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DEMOGRAPHIC ANALYSIS OF A UTAH-IDAHO

COYOTE POPULATION

by

Jeffrey J. Knudsen

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Science

UTAH STATE UNIVERSITY
Logan, Utah

1976

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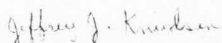

Jeffrey J. Knudsen

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	ii
LIST OF TABLES	vii
LIST OF FIGURES	x
ABSTRACT	xiii
INTRODUCTION	1
METHODS	3
Study Area	3
Population Measurement	8
Relative Density Indices	8
Absolute Density Estimates	11
Carcass Collection and Autopsy Procedures	11
Reproductive Analyses	12
Age Distributions	13
Tagging and Telemetry	15
RESULTS	16
Natality	16
Uterine Characteristics	17
Ovarian Measurements	23
Follicular Structures	24
Ovulation Frequencies and Pregnancy Rates	32
Breeding Dates	41
Litter Size	43
Total Reproductive Rate	46
Sex Ratios	47
Age Distributions	50

TABLE OF CONTENTS (Continued)

	Page
Modifications of Age Criteria.	50
Analyses for Possible Biases.	75
Age Composition of Curlew Valley Coyotes. .	94
Population Density.	94
Relative Population Trends	94
Absolute Density Estimates	106
Mortality	118
Annual Fall-to-Fall Population Mortality . .	118
Birth-to-Fall Pup Mortality	129
DISCUSSION	133
Techniques Review and Evaluation.	133
Natality	133
Annulus Formation	135
Age Assignment	136
Temporal Variation of Age Ratios.	138
Population Density	139
Mortality Rates	140
Coyote Densities	141
Onset of Reproductive Activity Between Years . . .	145
Reproductive Rates	147
Ovulation Frequency	147
Pregnancy Rates	149
Litter Sizes	151
Factors Influencing Coyote Reproductive Rates . . .	151
Age Ratios	158
Mortality Rates	163
Annual Fall-to-Fall Population Mortality	
Rates	163
Birth-to-Fall Pup Mortality Rates	167

TABLE OF CONTENTS (Continued)

	Page
Analyses of Demographic Patterns	175
2-3-Year Population Simulation	182
Summary.	186
LITERATURE CITED	191

LIST OF TABLES

Table	Page
1. Number of Coyote Carcasses Obtained Between September and April from Different Collection Sites and Years	13
2. Percentage of Female Coyotes in Northern Utah and Southern Idaho With Corpora Albicantia Which Also had Recognizable Placental Scars	22
3. Changes in Ovarian Size in Northern Utah and Southern Idaho Coyotes Between December and February . . .	25
4. Changes in Follicular Diameter Between December and February of Northern Utah and Southern Idaho Coyotes	27
5. Numbers and Diameters of Corpora Lutea of Northern Utah and Southern Idaho Coyotes	31
6. Number of Corpora Albicantia in Northern Utah and Southern Idaho Coyotes in Winters of 1972-73 and 1973-74	32
7. Percentage of Northern Utah and Southern Idaho Female Coyotes Ovulating, 1972-74	33
8. Percentage of Northern Utah and Southern Idaho Female Coyotes Pregnant, 1972-74	39
9. Estimates of Mean Litter Sizes in Northern Utah and Southern Idaho Coyotes, 1972-74	45
10. Sex Ratios of Coyote Populations in Curlew Valley and Vicinity, Winters of 1972-73 and 1973-74 combined .	49
11. Age Distributions of Coyotes Collected in Winter in Curlew Valley and Vicinity	74
12. Monthly Age Ratios of Coyotes Collected in Winter in Curlew Valley and Vicinity	78

LIST OF TABLES (Continued)

Table	Page
13. Movements (Inter-or-Intra-State) of Tagged Coyotes Between Initial Capture and Subsequent Recovery, 1972-75.	81
14. Age-Specific Coyote Vulnerability as Reflected by Transmitter Recovery Rates (Winters 1972-73 and 1973-74 Combined)	88
15. Calculated Spring Denning Indices for the Curlew Valley Study Area, 1972-74	95
16. Calculated Fall Trapping Indices for the Curlew Valley Study Area, 1972-74	96
17. Calculated Fall Scat Indices for the Curlew Valley Study Area, 1972-74	97
18. Relative and Composite Index Values, With Associated Standard Deviations and 95 Percent Confidence Intervals, for the Curlew Valley Coyote Population, 1972-74	98
19. Estimated numbers of coyotes in the Curlew Valley Study Area in May, 1972-74	113
20. Estimated Numbers of Coyotes in May (1972-1974) in the Curlew Valley Study Area Based on the Relationship Between the Pooled Composite Index Values and the Pooled Absolute Density Estimates	116
21. Procedure for Estimating Fall-to-Fall Population Mortality Rates for Curlew Valley Coyotes, 1972-73 and 1973-74	119
22. Causes of Coyote Mortality in Curlew Valley Based on Ear Tag, Transmitter, and Collar Recoveries from Coyotes that were Trapped and Released During the Three Falls 1972-74 and May 1973. Recoveries have been Recorded Through Winter 1974-1975	124

LIST OF TABLES (Continued)

Table	Page
23. Monthly Distribution of Deaths Among Ear-Tagged and Transmitted Curlew Valley Coyotes, 1972-74	128
24. Procedure for Estimating Birth-to-Fall Pup Mortality Rates in Curlew Valley, Summers 1973 and 1974	131
25. Coyote Densities in Curlew Valley and Other Areas .	142
26. Comparison of Ovulation Frequencies for Coyote Populations in Various Areas	148
27. Comparison of Pregnancy Rates for Coyote Populations in Various Areas	150
28. Coyote Litter-Size Comparisons in Various Areas .	152
29. Comparison of Coyote Winter Age Ratios	160

LIST OF FIGURES

Figure	Page
1. Location of Curlew Valley study area and carcass collection areas	5
2. Coyote uteri at various stages of reproductive activity. Early proestrus (December) on left through estrus (February) on right	19
3. Full-term placental scars as observed in an "opened" uterus	21
4. Sequence of follicular development from early proestrus (A) through early estrus (D), corpus luteum formation (E), terminating in corpus albicans formation (F). Millimeter scale at bottom	29
5. Conception dates estimated by aging fetuses from ten pregnant females in the winter carcass collections .	42
6. Measurements and ratios evaluated in pup-adult separation schemes (canine cross section at the gum-line)	52
7. Pattern of decreasing pulp-cavity sizes as coyotes age. Pup (left), yearling (middle), adult (right). Millimeter scale at bottom	54
8. Histogram of pulp-cavity length-tooth cross-sectional length ratios	57
9. Canine section (67X) of a 2 1/2 year-old coyote (1 x + 1 classification) and cementum measurement scheme. Tip ratio = $\frac{a}{b}$. Side ratio = $\frac{c}{d}$. Mean ratio = $\frac{\frac{a}{b} + \frac{c}{d}}{2}$. (p = periodontal membrane, i = dentine-cementum interface)	59

LIST OF FIGURES (Continued)

Figure		Page
10.	Canine section (67X) of a yearling coyote (1 x classification) and cementum measurement scheme. Tip ratio = $\frac{a}{b}$. Side ratio = $\frac{c}{d}$. Mean ratio = $\frac{\frac{a}{b} + \frac{c}{d}}{2}$. (p = periodontal membrane, i = dentine-cementum interface)	61
11.	Mean tip and side canine cementum ratios (one-annulus coyotes)	65
12.	Mean tip and side lower first premolar cementum ratios (one-annulus coyotes)	67
13.	Canine section (67X) of a 4 1/2 year-old coyote (3 x + 1 classification) and cementum measurement scheme. Tip ratio = $\frac{a}{b}$. Side ratio = $\frac{c}{d}$. Mean ratio = $\frac{\frac{a}{b} + \frac{c}{d}}{2}$. (p = periodontal membrane, i = dentine-cementum interface)	70
14.	Canine section (67X) of a 2 1/2 year-old coyote (2 x + 1 classification) and cementum measurement scheme. Tip ratio = $\frac{a}{b}$. Side ratio = $\frac{c}{d}$. Mean ratio = $\frac{\frac{a}{b} + \frac{c}{d}}{2}$. (p = periodontal membrane, i = dentine-cementum interface)	72
15.	Relative denning indices	101
16.	Relative trapping indices for the three individual traplines and the combined trapline	102
17.	Relative scat-line indices	103

LIST OF FIGURES (Continued)

Figure	Page
18. Composite relative index values and accompanying 95 percent confidence intervals	105
19. Capture-recapture May pup population estimates. Brackets represent one standard deviation	114
20. Comparison of the two sets of absolute density esti- mates with the composite relative index values . .	115
21. Three-year simulation of Curlew Valley coyote population	183
22. Comparison of the estimated (capture-recapture) and simulated numbers of pups in May	187

ABSTRACT

Demographic Analysis of a Utah-Idaho

Coyote Population

by

Jeffrey J. Knudsen, Master of Science

Utah State University, 1976

Major Professor: Frederic H. Wagner

Department: Wildlife Science

I estimated various demographic parameters of the coyote population in Curlew Valley, northern Utah and southern Idaho, during the period August 1972 through September 1974. Field work provided estimates of relative and absolute coyote densities and established causes of coyote mortality. Laboratory analyses of 866 coyote carcasses supplied information on sex and age ratios, ovulation frequencies, pregnancy rates, and litter sizes.

Annual ovulation frequencies and pregnancy rates for the entire population varied from 70 to 92 percent and 57 to 88 percent respectively. Age-specific ovulation frequencies varied from 63 to 91 percent, respectively, for pups and adults. Similarly, age-specific pregnancy rates varied from 53 to 100 percent for pups and adults respectively. Mean age-specific litter sizes were 6.0, 5.9, 6.5, and 6.2 for pups,

yearlings, adults, and all ages combined. Reproductive rates appeared to be inversely related to coyote densities; hence, density-dependent processes operated in this population.

The sex ratio of denned pups (May) did not differ significantly from an expected 50:50 sex ratio. The pup sex ratio in the winter carcass collections differed significantly from 50:50 whereas that of yearlings and adults did not.

The percentage of pups varied from 42 to 56 percent in the winter carcass collections. Ages of coyotes were determined by counting cementum annuli in longitudinal canine and lower first premolar sections. In addition to the conventional method of assigning ages, I developed a second method based on cementum thickness ratios. This method was necessary since my collections were obtained during the period of annulus formation. Hence it is possible to observe coyotes of the same age that display different numbers of annuli.

Both the relative- and absolute-density data revealed substantial short-term variation in coyote densities. Post-whelping, May coyote densities may have varied from 1.5 to 0.2 coyotes per square mile (0.6 to 0.08 coyotes per km²).

The mortality of coyotes 5 months old and older was almost entirely man-induced. Annual fall-to-fall population mortality varied from 42 to 82 percent. Similarly, estimated birth-to-fall pup mortality rates ranged from 41 to 72 percent, with the major losses

probably occurring between birth and May. Coyotes are probably most susceptible to natural mortality during their first few months of life.

(210 pages)

INTRODUCTION

Coyote (Canis latrans) populations in northwestern Utah and southern Idaho have been shown to undergo short-term fluctuations in density (Clark 1972) as they do elsewhere in North America (Keith 1963; Gier 1968; Wagner 1972). These Utah-Idaho changes may be associated, at least in part, with food availability (Clark 1972), a conclusion also reached by Gier (1968) for Kansas coyotes. Lagomorph density in Clark's area, particularly of black-tailed jackrabbits (Lepus californicus) which constituted the greatest component of the coyote diet, varied greatly between years (Gross et al. 1974). Clark suggested that variation in reproductive rate was one of the demographic mechanisms responsible for fluctuations in coyote density. He lacked evidence on the role of mortality rates.

Long-term mean densities about which coyote populations fluctuate vary between areas (Knowlton 1972). These variations have been attributed to differences in food availability (Clark 1972) and to differences in artificial control (Knowlton 1972), especially the use of toxicants (Wagner 1972).

If we are to develop a thorough understanding of short-term fluctuations in coyote numbers as well as the pattern of influences determining long-term mean density, we must measure demographic and

movement characteristics and relate these to the environmental variables affecting them.

The present 2-year study (August 1972 to September 1974) was part of a long-term effort to study the population ecology of coyotes in Curlew Valley, an area in northwestern Utah and southern Idaho. Specifically, the objectives of this study were: (1) to develop techniques for measuring various demographic parameters; (2) to measure annual coyote densities, both absolute and relative, and reproductive and mortality rates; and (3) to determine causes and seasonal distribution of mortality. The interactions of these demographic parameters were synthesized to simulate changes in coyote density during the 2 years of this study, and the simulated and measured densities were then compared.

Throughout this paper I present statistical interpretations whenever possible. These results often indicate that there are no significant differences in these comparisons. Nevertheless, in many cases I extend my interpretations of these data beyond the statistical results. The inferences I draw from these sample data are my best estimates of the demographic patterns that occurred in this coyote population during my study. The results of the various statistical analyses permit the reader to objectively evaluate my interpretations. I emphasize that these interpretations are often based on small samples and that if larger samples had been obtained, my interpretations of these data may have been supported statistically. On the other hand, larger samples

may have, in some cases, suggested different interpretations. Similarly, these data, as presented, may be subject to different interpretations than the ones I present.

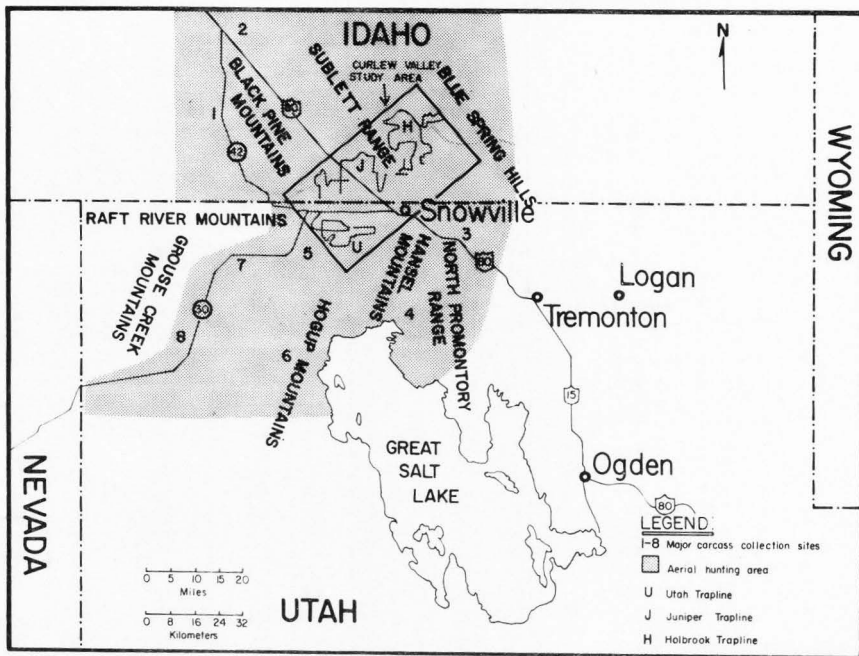
METHODS

Study Area

Curlew Valley, hereinafter termed "the valley," lies 60 miles (97 km) west of Logan, Utah in Box Elder County, Utah and Cassia and Oneida counties, Idaho (Figure 1). This intermountain basin (3,367 km²), once covered by Pleistocene Lake Bonneville (Flint 1947) is surrounded on three sides by mountains with maximum elevations ranging from 6388 feet (1,947 m) to 9924 feet (3,025 m), and on its southern side by the Great Salt Lake mud flats. Gross et al. (1974) gave a more detailed topographical description of the valley.

Climate and vegetation of the valley are characteristic of the Northern Desert Shrub Biome described by Fauntin (1946). The northern part of the valley receives an average of 12-14 inches (30-36 cm) of precipitation annually, the southern part receives half this amount. Most falls as rain in spring and fall, and as snow during the winter. Temperatures range from -32 C in January to 38 C in July, mean values for these 2 months are -6 C and 21 C respectively (Mitchell 1965).

Typically, vegetative associations are dominated by one or two plant species. The following approximate cover-type percentages for



the study area were estimated by Stephen Hoffman (Personal Communication): 45 percent big sagebrush (Artemisia tridentata); 8 percent shadscale (Atriplex confertifolia); 8 percent shadscale-sagebrush mixture; 3 percent greasewood (Sarcobatus vermiculatus) with some plants of this species associated with either sagebrush or shadscale; and 10 percent juniper (Juniperus osteosperma) primarily on the foothills and lower mountains. The northern portions of the study area contain scattered stands of aspen (Populus tremuloides) and Douglas fir (Pseudotsuga menziesii) which together cover less than 1 percent. Gross et al. (1974) provide further vegetative descriptions of Curlew Valley.

The major agricultural crops, winter wheat (Triticum aestivum) and alfalfa (Medicago sativa), are grown largely in the Idaho portion of the study area, and occupy about 15 percent of its total area. An additional 10 percent has been cleared and seeded to crested wheat grass (Agropyron desertorum) for livestock grazing.

Most of the study area is open to grazing by sheep, mainly in winter, and cattle on a year-round basis. Approximately 60 percent of the study area is controlled by the U. S. Bureau of Land Management and the U. S. Forest Service. The remaining 40 percent is privately owned.

Carnivores other than coyotes which inhabit the valley are bobcats (Lynx rufus), long-tailed weasels (Mustela frenata), striped

skunks (Mephitis mephitis), kit fox (Vulpes macrotis), red fox (Vulpes fulva), and an occasional mountain lion (Felis concolor). The four species of lagomorphs present are black-tailed jackrabbits, white-tailed jackrabbits (Lepus townsendi), mountain cottontails (Sylvilagus nuttalli), and pygmy cottontails (Sylvilagus idahoensis). Stephen Hoffman (Personal Communication) reports 23 species of rodents in the valley. The four most abundant rodent species are deer mice (Peromyscus maniculatus), Great Basin pocket mice (Perognathus parvus), Ord's kangaroo rats (Dipodomys ordi), and least chipmunks (Eutamias minimus). Mule deer (Odocoileus hemionus) and pronghorn antelope (Antilocapra americana) occur in the valley.

Numerous passerines and small ground-nesting birds, 7 species of galliforms, and 13 of raptors nest in the valley. Reptiles are represented by 6 species of snakes and 9 of lizards.

The 700 square mile ($1,813 \text{ km}^2$) Curlew Valley study area (Figure 1) hereinafter termed "the study area," lies within the valley (Clark 1972) with approximately 40 percent in Utah and 60 percent in Idaho. All population indices and estimates were made in this area, and all tagged and transmittered animals were originally caught here. However, because large samples were needed I obtained carcasses from coyotes shot over a wider area surrounding the study area. The inferences I draw about population dynamics are intended explicitly for the study area; but, the reproductive, sex and age composition, and mortality conclusions derive from the carcass collections. The implication is

therefore present that conclusions drawn for the study area apply more broadly to the shaded area shown in Figure 1.

Population Measurement

Relative Density Indices

Information on population trend was derived from three relative indices (Clark 1972).

Denning: Dens were located in mid-May in the study area from the air using a Piper Supercub 135 aircraft. Wayne Larsen piloted while Milton Robinson scanned the ground for dens in the mornings when air conditions permitted slow, low-elevation flight. Active (pups or adults seen) or suspected dens, were described with respect to landmarks; or in areas of uniform terrain, marked with lengths of toilet paper dropped in the vicinity. Dens were dug out the day they were located and the litters captured.

Litter size, sexes, and general condition of the pups were noted. Ear tags were placed in both ears prior to their release into what remained of the den. The purpose of the denning was two-fold. Number of dens found per flying hour served as a relative index to spring pup densities, and the ear-tagged pups comprised the marked sample of a capture-recapture population estimate.

Trapping: In each of the three autumns (1972 to 1974), 150 No. 3 double-spring Oneida-Victor steel traps were set for 30 days. Clark

(1972) randomly selected permanent trap-site locations early in his study by numbering the 700 square miles of the study area consecutively and drawing 150 of these numbers at random. He modified the trapline after the first year due to severe logistical problems encountered while checking the traplines. The modified traplines were situated along networks of roads within the study area. Traps were placed as much as possible at the same locations each year thereafter. Since roughly two-thirds of the study area lies in Idaho, two lines of 50 traps each were located in Idaho, and a third was placed in the Utah portion (Figure 1).

Traps were set against a backdrop of sagebrush or some other natural object so as to restrict a coyote's angle of approach to the set. Sets were initially scented with a beaver-based scent and rescented 2 weeks later with coyote urine. Each line was checked daily by one of the three men involved in this phase of the project.

The use of tranquilizer tabs minimized foot damage (Balser 1965). Tabs were made by applying a 1/8-inch (3 mm) layer of white petroleum jelly, forming a circle of roughly 3 inches (7.5 cm) diameter, to the center of a 4-inch² (10-cm²) section of four-layer gauze. The powdered tranquilizer was placed in the center of the gauze. The corners were gathered until the ball of gauze, petroleum jelly, and tranquilizer were about 3/4 inch (2 cm) in diameter. A 10-inch (25.4-cm) piece of wire was used to tie off the ball and the excess gauze tails were cut off. The tabs were then dipped in melted paraffin three or four times, and

attached to a jaw of the trap with the wire. While in the trap, coyotes chewed the tabs and ingested some of the tranquilizer.

Due to shortages a different tranquilizer was used each fall: Diazepam, Vetame, and Tranvet. Dosage levels varied from 250 to 450 mg depending on brand. Coyote weights varied from 9-32 lbs. (4.1-14.5 kg), necessitating compromise dosages. Effects of the drug lasted for 24-72 hours depending on coyote weight and amount of drug ingested. Each animal was cared for at the University field station in Snowville, Utah until the effects had worn off, and then released at the point of capture. While at the field station sex, age, and weight were obtained and they were ear-tagged and collared with radio transmitters.

The fall trapping served several purposes: (1) the number of coyotes caught per 1000 trap days was used as a relative index of abundance; (2) the captured, spring-tagged pups yielded the second sample of a capture-recapture density estimate; and (3) coyotes tagged and/or instrumented with radio transmitters facilitated survival studies.

Scat index: Each year in early November, L. Charles Stoddart cleared a standard 40-mile (64-km) route of dirt roads within the Utah portion of the study area of coyote droppings (scats). At the end of two 2-week intervals thereafter, he gathered and counted coyote scats along this route. The number of scats per week was used as a second, relative index of fall densities.

Absolute Density Estimates

In combining spring denning and fall trapping data for capture-recapture estimates of spring pup densities, Bailey's (1952) adjusted formula for small sample sizes was used because it provides both density estimates and a means of calculating standard deviations for small sample sizes like those obtained in this study. December age ratios obtained from the carcass collections allowed conversion to total population densities.

Carcass Collection and Autopsy Procedures

During the winters of 1972-73 and 1973-74, coyote carcasses were obtained for autopsy. In addition, the 1970-71 carcass collection, obtained prior to my study, was made available to me.

Most carcasses were obtained from a group of sheep ranchers operating out of Tremonton, Utah who shot coyotes on sheep winter range from planes. They hunted in, and to the south of, the study area (all in Box Elder County, Figure 1) usually beginning in December and ending in February. Major collections were made during January when snow cover and visibility were favorable. I provided the gunners with tags so they could attach the date and location of kill to each carcass. I also obtained some carcasses from Division of Wildlife Service personnel when they conducted aerial gunning operations in Idaho (sites 1 and 2, Figure 1). In addition to the aerial-gunned coyotes, each year

some carcasses were obtained from ranchers and other individuals who shot coyotes within the study area. Over half of those collected during 1973-74 were from the latter sources. Numbers of carcasses received from each collecting site and vicinity (Figure 1) are summarized in Table 1.

When time permitted (from 1 to 6 months after collection), carcasses were thawed, gross autopsies performed, and sex and carcass weights recorded. Stomachs, skulls, and female reproductive tracts were removed and refrozen (uteri in water to prevent dehydration). Tissues and organs were labelled with the respective autopsy numbers of the animals from which they had been taken.

Reproductive Analyses

Carcasses were collected during proestrus and estrus, thus affording the opportunity to observe ovarian and follicular changes during these periods. These observed changes allowed determination of breeding status and provided data for determining the onset of reproductive activity.

Each ovary was removed from the infundibulum and stored in formalin for several days prior to examination. At the time of analysis, a dissecting microscope with an ocular scale was used to measure ovarian lengths and diameters to the nearest 0.1 mm. Each ovary was sliced into 5 or 6 thin, longitudinal sections with a razor blade.

Table 1. --Number of Coyote Carcasses Obtained Between September and April from Different Collection Sites and Years

Site ¹	No. Carcasses Collected by Year		
	1972-73	1973-74	2-year totals
1	--	13	13
2	--	17	17
3	--	19	19
4	--	15	15
5	23	13	36
6	109	40	149
7	24	--	24
8	41	5	46
5 or 6	59	--	59
6 or 8	104	--	104
7 or 8	--	43	43
Study area	56	104	160
Totals	416	269	685

¹ See Figure 1

Maximum follicle size and numbers and size of corpora lutea and corpora albicantia were recorded.

Uterine horns were opened and examined for placental scars. Reproductive tracts of carcasses collected in February, March, and April were examined for signs of pregnancy. The number of implantation sites and/or fetuses were recorded.

Age Distributions

Mortality-rate calculations for the entire population and for pups during the first 5 months of life were based on pup-adult age ratios at various times of the year. Hence, age distributions were determined in

each year of this study. Linhart and Knowlton (1967) reviewed techniques for determining ages of coyotes and presented their findings on age determination by counting cementum annuli in coyote canines. The procedure I followed was similar to theirs; however, I used a different decalcification procedure and two additional stains.

Canines were decalcified in a 5 percent nitric acid (71 percent) solution prepared in sufficient volume to allow 100 ml per tooth. Solutions were changed every 12 hours until decalcification was complete (24 to 48 hrs.). To check for decalcification, equal volumes (1 ml) of 5 percent ammonium hydroxide, 5 percent ammonium oxalate, and decalcification solution were mixed. A cloudy mixture indicated incomplete decalcification, whereas a clear mixture indicated the process was complete. Once decalcified, the teeth were rinsed in running water for at least 12 hours (David Beale, Personal Communication).

Using a razor blade, I severed tooth crown from root at the gum line and obtained length and width measurements of the cross-sectional aspects of both pulp cavity and tooth. A dissecting microscope was used to obtain measurements to the nearest 0.1 mm. Pulp-cavity cross-sectional measurements and the ratios between pulp-cavity cross-sectional measurements and corresponding tooth cross-sectional measurements were plotted to separate pups from older coyotes. This separation reduced by half the number of canines requiring sectioning and staining for determination of age distributions.

Longitudinal root sections 16μ thick were obtained with a cryostat (Model CTD, International Equipment Company). All sections for a particular coyote were placed on one slide prior to staining.

Of the seven stains evaluated, three were finally chosen: paragon, toluidine blue, and crystal violet. Since, in some instances, one stain worked better than the others, it seemed desirable to stain three or four sections each with a different stain. The stain was eye-dropped onto the sections and washed off after 5 or 6 seconds. Staining was repeated until the desired staining darkness was obtained. The slide and stained sections were dried on a slide warmer (40 to 50 C) and mounted in Namount.

As needed, additional canines and eventually lower first premolars and incisors were sectioned until a clear annulus count was obtained. To test for aging agreement, sets of lower canines, lower first premolars, and lower incisors were taken from 43 coyotes. Paired lower canines and lower first premolars had the same number of annuli in 83 percent of the counts. In the case of animals with one or more annuli 73 percent agreement was obtained. Canine and premolar counts were much more reliable than incisor counts. I used canines in assigning 73 percent of the ages, premolars for 27 percent.

Tagging and Telemetry

The numbered ear tags placed in both ears of fall-trapped and spring-denned coyotes had a return address on them, as did the

transmitter collars. Tag returns were used for two purposes: (1) to obtain information on causes of coyote mortality, and (2) the first-winter return rate provided an index of over-winter mortality rates.

Tag returns were biased toward mortality associated with human activities (Clark 1972). For this reason telemetry was used in an attempt to document all causes of mortality. Transmitter return rates also gave insight into over-winter mortality rates. The transmitters were designed (Kolz et al. 1973), constructed, and supplied by personnel of the Denver Wildlife Research Center. It was possible to detect mortality cases within 4 hours after death with them. Hibler (1976) gave a comprehensive description of techniques and facilities used in the combined movement and survival telemetry studies.

RESULTS

Nativity

While the proestrus and estrus periods typically span about 10 and 6-10 days, respectively, in the domestic dog (Asdell 1946; Nalbandov 1964; Turner and Bagnara 1971), they apparently persist for about 60-90 and 9.5 days in the coyote (James Kennelly, Personal Communication). The duration of proestrus was based primarily on the presence of blood in the vaginal washings (Ibid.).

Winter carcass collections in the present study allowed analysis of ovarian and follicular changes during these periods which could be

used for comparing the timing of reproductive activity between years and estimating ovulation frequencies and pregnancy rates.

Uterine Characteristics

The most obvious uterine change during proestrus and estrus is the pronounced size increase during the winter (Figure 2) evident in pups, yearlings, and adults. Pups are here defined as animals between birth and 1 year of age. Yearlings are defined as animals between 1 and 2 years of age, adults are 2 years old or older.

I examined uteri from yearling and older females in the winter carcasses for the presence of placental scars (Figure 3) in order to estimate both the proportion of females bearing young the previous spring and age-specific litter sizes. Since I examined ovaries from these same females for the presence of corpora albicantia, in order to estimate ovulation frequencies, I was able to compare the incidence of both scars and corpora in the same animals (Table 2).

Such a comparison involves two assumptions. First, a coyote that ovulates and implants will have both corpora albicantia and placental scars in the early weeks of the following winter. Second, those coyotes which ovulate but fail to implant will have corpora albicantia but will lack placental scars in the following winter.

Figure 2. Coyote uteri at various stages of reproductive activity.
Early proestrus (December) on left through estrus (February) on right.

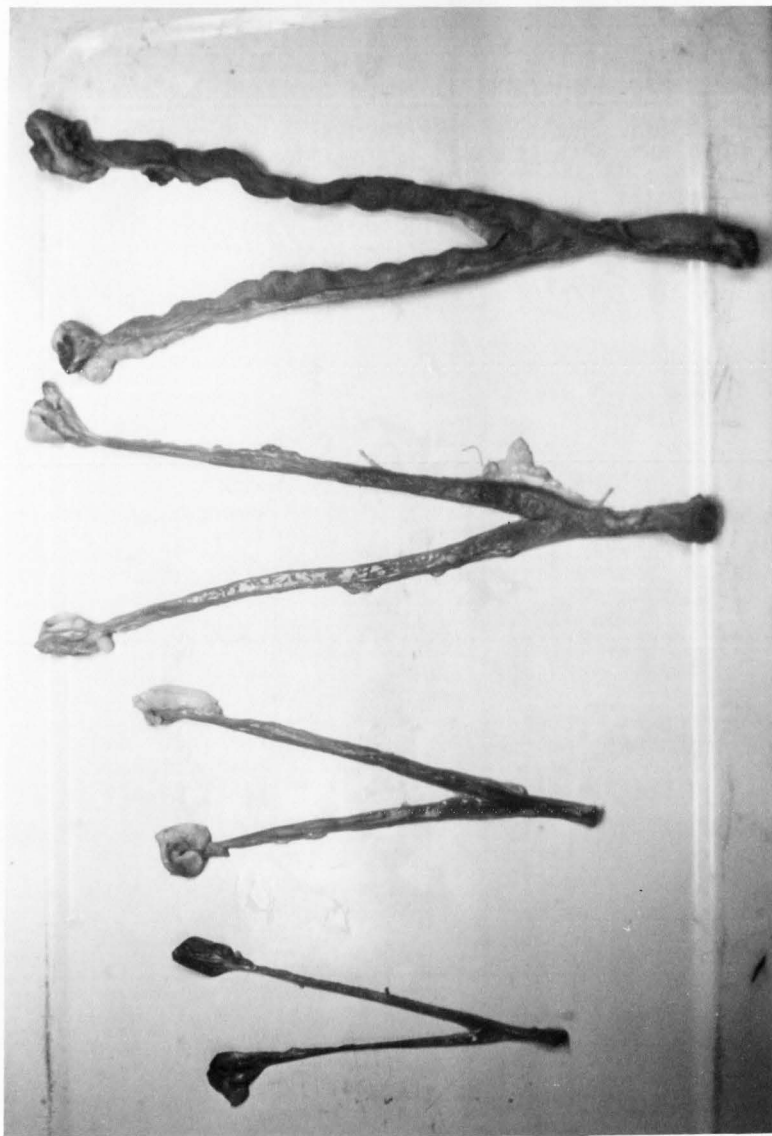


Figure 3. Full-term placental scars as observed in an "opened" uterus.

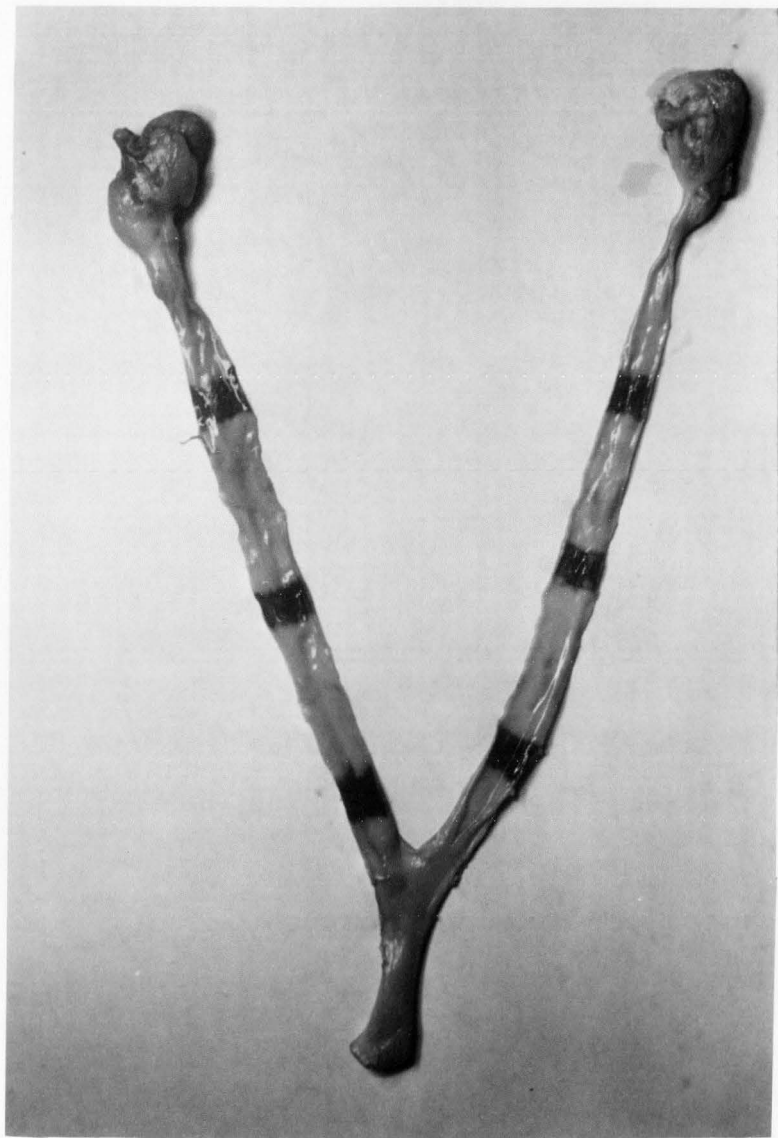


Table 2.--Percentage of Female Coyotes in Northern Utah and Southern Idaho With Corpora Albicantia Which Also had Recognizable Placental Scars

Winter	Percent with Scars, 90% Conf. Int., and (Sample Size) by Date			
	Dec.	1-19 Jan.	20-31 Jan.	Feb.
1972-73	75,50-90 (12)	50,27-73 (12)	17,2-54 (6)	57,30-83 (7)
1973-74	100,62-100 (5)	67,40-85 (12)	67,20-96 (3)	75,32-97 (4)
Totals	82,64-93 (17)	58,41-74 (24)	33,13-61 (9)	64,32-83 (11)

The mean proportion of females with corpora which also had scars was 82 percent in December (Table 2) suggesting that as many as 18 percent of the females ovulated but failed to successfully implant in the 2 years. The confidence intervals for the four chronological groups in Table 2 all overlap. Hence, these data do not suggest a statistically significant decrease in placental scar clarity during the winter. Nevertheless, based on my analyses of numerous reproductive tracts, I suggest that placental scars tend to be obscured as uterine activity for the next breeding season increases. For this reason placental-scar counts from late-winter carcass collections should be interpreted with care, and I have used only the December samples to estimate pregnancy rates of the previous spring.

Ovarian Measurements

Since uterine activity and growth are stimulated by ovarian hormones, particularly estrogen and progesterone (Turner and Bagnara 1971), the onset of ovarian activity must precede the onset of uterine activity. Hence, changes in ovarian size should reflect the onset of reproductive activity in any particular year and are perhaps a more sensitive indicator than uterine changes in early winter.

After storage in formalin for several days, maximum length and diameter of each ovary was obtained with a dissecting microscope and ocular scale. Neither right and left lengths, nor right and left

diameters differed statistically within pups or yearlings. Consequently, respective right and left ovarian measurements were combined within each age group. Right ovaries were significantly larger in adults, but respective right and left ovarian measurements were combined nevertheless.

Ovarian size increased as the winters progressed (Table 3). Of the 16 pup and yearling comparisons between years, two mean ovarian values were significantly greater in the second winter than in the first as was evidenced by non-overlap of their respective 90 percent confidence intervals (Table 3). Thus, in a statistical sense, there was no difference in the onset of reproductive activity as reflected by ovarian dimensions in these two age classes between years. It was not possible to test for between-year differences in the adult age class since I combined respective right and left measurements even though they were significantly different as previously mentioned. Therefore the combined adult measurements are not normally distributed. Nevertheless, I suspect that reproductive activity may actually have begun earlier the second winter since respectively, 75, 88 and 62 percent of the pup, yearling, and adult mean ovarian values were larger.

Follicular Structures

I measured the diameter of the largest follicle in each ovary. The mean of these increased from 0.5 mm in December to 4.0 mm in

Table 3.--Changes in Ovarian Size of Northern Utah and Southern Idaho Coyotes Between December and February

		Mean in mm, 90% Conf. Int. or Std. Dev. and (Sample Size ¹) by Date							
Age	Dimension	Winter 1972-73				Winter 1973-74			
		Dec.	1-15 Jan.	16-31 Jan.	Feb.	Dec.	1-19 Jan.	20-31 Jan.	Feb.
Pup ²	Diameter	5.6 ± 0.52 (14)	7.2 ± 0.53 (18)	7.4 ± 0.70 (22)	8.9 ± 0.67 (11)	7.8 ± 1.04 (8) ³	7.9 ± 1.00 (8)	7.6 ± 1.15 (8)	7.2 ± 0.53 (34)
	Length	10.2 ± 0.74 (14)	11.6 ± 0.88 (18)	11.6 ± 0.68 (22)	12.9 ± 1.20 (11)	12.5 ± 1.00 (8) ³	12.1 ± 1.53 (8)	11.9 ± 0.92 (8)	11.9 ± 0.58 (34)
Yearling ²	Diameter	7.7 ± 1.03 (11)	8.0 ± 0.70 (12)	7.8 ± 0.83 (12)	9.6 ± 0.93 (8)	7.8 ± 0.62 (2)	8.7 ± 0.77 (12)	9.4 ± 1.69 (6)	11.2 ± 1.40 (6)
	Length	11.4 ± 0.70 (11)	12.4 ± 0.95 (12)	12.5 ± 0.93 (12)	12.9 ± 1.90 (8)	14.0 ± 5.67 (2)	12.4 ± 0.89 (12)	14.4 ± 2.33 (6)	15.8 ± 2.50 (6)
Adult ⁴	Diameter	7.4 ± 1.18 (14)	8.0 ± 1.74 (16)	8.6 ± 1.36 (5)	9.9 ± 1.56 (7)	9.6 ± 1.03 (8)	9.8 ± 1.64 (12)	8.0 ± 2.12 (2)	10.6 ± 2.28 (8)
	Length	12.1 ± 1.61 (14)	12.7 ± 2.70 (16)	11.6 ± 0.96 (5)	15.3 ± 2.12 (7)	13.0 ± 1.82 (8)	14.6 ± 1.24 (12)	11.4 ± 0.21 (2)	14.6 ± 1.72 (8)

¹ One coyote provides two samples

² Mean values and 90 percent confidence intervals

³ Mean value is significantly larger than in previous winter at the 90 percent level

⁴ Mean values ± one standard deviation, see text for explanation

February (Table 4) whereas individual follicle measurements varied from 0.1 mm in December to 5.5 mm in February. The latter agrees closely with mature follicle sizes of 6.0 and 7.0 mm given by Mossman and Duke (1973) for domestic dog and fox respectively. The results in Table 4 do not include follicle measurements from those coyotes which had already ovulated (as indicated by the presence of corpora lutea), since the remaining follicles probably were already ^{atrophy?} atrofying. This explains the small sample sizes or lack of data for some of the late January and February categories. Figure 4 shows a sequence of follicular development terminating in corpus albicans formation.

Clark (1972) assumed that once a follicle attained a diameter of 2.0 mm it was destined to mature and rupture. My data support this assumption. The results in Table 4 are summarized for two ranges of follicle size with 2.0 mm serving as the point of separation. Increased follicle size is first noticeable in the early January collections. As winter progresses there is an increasing disparity between the sizes of inactive and maturing follicles. This separation scheme should not be considered as a discrete separation of active and inactive follicles, especially early in the winter as many of those coyotes placed in the 0-1.9 mm range will undoubtedly develop mature follicle later in the winter. This scheme is probably most reliable in late January and February since the greatest separation of follicle sizes occurs at this time. Most inactive follicles, even in late January and February, remain at about 1 mm in diameter whereas maturing follicles are

Table 4. Changes in Follicular Diameter Between December and February of Northern Utah and Southern Idaho Coyotes

Mean Follicle Diam. in mm, 90% Conf. Int., and (Sample Size ¹) by Date										
Age	Follicle Diameter	Winter 1972-73				Winter 1973-74				
		Dec.	1-15 Jan.	16-31 Jan.	Feb.	Dec.	1-19 Jan.	20-31 Jan.	Feb.	
Pup	0-1.9	0.5 ± 0.11 (13)	0.9 ± 0.18 (14)	1.1 ± 0.20 (15)	0.4 ± -- (1)	0.8 ± 0.45 (6)	1.2 ± 0.33 (8)	1.3 ± 0.32 (7)	0.8 ± 0.16 (27)	
	≥ 2.0	--	3.1 ± 0.79 (4)	3.9 ± 0.90 (4)	4.0 ± 0.74 (3)	--	--	--	2.1 ± -- (1)	
Yearling	0-1.9	0.6 ± 0.14 (9)	1.0 ± 0.12 (10)	0.9 ± 0.36 (7)	1.0 ± -- (1)	1.0 ± -- (2)	1.2 ± 0.14 (10)	1.2 ± 0.80 (4)	--	
	≥ 2.0	--	--	3.2 ± 0.91 (7)	4.0 ± -- (1)	--	2.8 ± 1.25 (2)	3.9 ± 1.25 (2)	--	
Adult	0-1.9	0.8 ± 0.17 (13)	1.1 ± 0.26 (8)	1.1 ± 0.20 (3)		1.3 ± 0.19 (8)	1.4 ± 0.22 (6)	1.2 ± 0.31 (2)	1.6 ± -- (1)	
	≥ 2.0	--	2.6 ± 0.62 (2)	2.0 ± -- (2)	2.8 ± 4.73 (2)	--	3.2 ± 1.56 (2)	--	2.3 ± -- (1)	

¹ One coyote provides two samples

Figure 4. Sequence of follicular development from early proestrus (A) through early estrus (D), corpus luteum formation (E), terminating in corpus albicans formation (F). Millimeter scale at bottom.



substantially larger than 2.0 mm. For this reason I will make the same assumption as Clark which applies only to late-winter carcass collections in which reproductive activity has progressed sufficiently to ensure follicular development. Late-breeding coyotes may be classified as non-ovulators by this scheme if their follicles are less than 2.0 mm in the February collections. The 90 percent confidence intervals overlap between all possible age-specific comparisons between years. Hence it is not possible to show a statistical difference in the timing of reproductive activity between years. Nevertheless, nearly all mean follicle diameters were larger the second year than in the first year, which suggests that the onset of reproductive activity may have occurred somewhat earlier in the second year.

The corpus luteum is larger than a mature follicle and is the dominant structure in the ovary during pregnancy (Table 5, Figure 4). The importance of corpus luteum in ovulation-frequency estimation will be discussed in a later section.

I recorded the numbers of corpora albicantia when present. Mansell (1971) recognized more than one set of corpora albicantia in white-tailed deer, suggesting that in this species they persist for several years. Similarly, in recent work on bobcats, Crowe (1975) reported that female bobcats may never lose corpora albicantia and some older females had up to 59 corpora. In only one or two instances did I suspect more than one set of corpora albicantia and even this was not

Table 5. --Numbers and Diameters of Corpora Lutea of Northern Utah and Southern Idaho Coyotes

Mean No. per Coyote, Diam., 90% Conf. Int., and (Sample Size) by Winter				
Age	Winter 1972-73		Winter 1973-74	
	No.	Diam. (mm)	No.	Diam. (mm)
Pup	11.0 ± 6.30 (2)	6.4 ± 0.70 (5)	7.7 ± 3.51 (3)	6.8 ± 0.36 (6)
Yearling	5.8 ± 1.76 (4)	6.6 ± 0.57 (9)	5.8 ± 2.61 (4)	7.0 ± 0.46 (8)
Adult	9.0 ± 6.07 (3)	6.6 ± 0.72 (8)	6.2 ± 0.59 (13)	6.6 ± 0.43 (26)
Ages combined	8.0 ± 1.91 (9)	6.6 ± 0.33 (22)	6.0 ± 0.82 (20)	6.7 ± 0.29 (40)

certain. In general, as in the red fox (Layne and McKeon 1956), corpora albicantia do not appear to persist for more than 1 year.

Table 6 presents the mean numbers of corpora albicantia for the two winters combined. The coyotes' ages each winter were corrected back to the appropriate ages of the previous breeding season--for example, a coyote aged as a yearling in a winter carcass collection was actually a pup at the time of ovulation. Clarity of corpus albicans decreased as the winters progressed due to the presence of maturing follicles and corpora lutea; however, they were still apparent in the February collections. Since I am interested only in whether or not an animal ovulated, corpus-albicans data from all months of the winter carcass collections were used for inferring ovulation frequencies.

Table 6. -- Numbers of Corpora Albicantia in Northern Utah and Southern Idaho Coyotes in the Winters of 1972-73 and 1973-74

Age	Mean No. per Coyote, 90% Conf. Int. and (Sample Size) of Corpora by Date			
	Dec.	1-19 Jan.	20-31 Jan.	Feb.
Pup	6.0 \pm 12.64 (2)	5.0 \pm 1.56 (6)	4.0 \pm 1.68 (3)	4.5 \pm 9.46 (2)
Yearling	4.0 \pm 12.64 (2)	5.3 \pm 1.69 (6)	5.0 \pm -- (1)	10.0 \pm -- (1)
Adult	10.7 \pm 2.31 (6)	7.8 \pm 1.48 (4)	8.5 \pm 3.17 (2)	5.3 \pm 5.41 (3)
Ages combined	8.4 \pm 2.25(10)	5.8 \pm 0.91(16)	5.7 \pm 1.92(6)	5.8 \pm 2.52 (6)

Ovulation Frequencies and Pregnancy Rates

I determined ovulation frequencies (percentage of females ovulating, Table 7) on the basis of coyotes that had ovulated, as shown by the presence of corpora lutea, or that had large follicles (2.0 mm or larger). Over estimation might occur if some coyotes in the "probable ovulation" category fail to ovulate, and underestimation might occur if some coyotes were destined to develop mature follicles and ovulate later than the last collections. Additional ovulation-frequency estimates were obtained from the proportion of females in the winter carcass collections which had corpora albicantia.

I subdivided the ovulation-frequency data by year and age class (Table 7). In addition, I combined age classes in each month's sample to obtain estimates of total-ovulation frequencies ("overall" category, Table 7) by two methods. In the first, this category was based on a

Table 7. --Percentage of Northern Utah and Southern Idaho Coyotes Ovulating, 1972-74

Breeding season	Data source	% Ovulating, 90% Conf. Int., and (Sample Size) by Age Class				Wtd. Mean % Ovulating ³ and Std. Dev.
		Pup	Yearling	Adult	Overall ²	
1972	Corpus albicans samples	62, 42- 77 (26)	86, 64- 96 (14)	70, 35- 88 (10)	70, 58- 81 (50)	74 ± 7.09
1973	Corpus albicans samples	65, 36- 78 (17)	100, 46-100 (3)	93, 74- 99 (14)	76, 66- 88 (34)	88 ± 3.66
	Feb. samples	36, 16- 59 (14)	71, 32- 92 (7)	100, 62-100 (5)	58, 37- 77 (26)	69 ± 8.54
	Mar-Apr samples ¹	100, 10-100 (1)	100, 62-100 (5)	100, 10-100 (1)	100, 68-100 (7)	100 + --
	Combined samples	67, 46- 84 (18)	87, 67- 96 (15)	95, 80-100 (20)	83, 73- 91 (53)	84 ± 5.14
1974	Feb. samples	12, 3- 29 (17)	100, 46-100 (3)	100, 62-100 (5)	40, 22- 62 (25)	81 ± 1.69
	Mar-Apr samples	100, 32-100 (2)	50, 14- 86 (1)	100, 80-100 (11)	88, 66- 98 (17)	88 ± 6.25
	Combined samples	100, 32-100 (2)	71, 32- 92 (7)	100, 85-100 (16)	92, 79- 98 (25)	93 ± 4.29
2-3 year totals	Corpus albicans samples	60, 46- 73 (43)	88, 71- 97 (17)	83, 68- 92 (24)	73, 63- 81 (84)	79 ± 4.54
	Feb. samples	22, 10- 37 (31)	80, 50- 94 (10)	100, 78-100 (10)	49, 36- 64 (54)	74 ± 4.81
	Mar-Apr samples	100, 46-100 (3)	78, 49- 94 (9)	100, 82-100 (12)	92, 75- 98 (24)	92 ± 4.86
	Combined samples	63, 50- 76 (46)	83, 70- 93 (36)	91, 80- 97 (46)	79, 72- 85 (128)	81 ± 3.16

¹ Based on Corpus albicans + Mar. -April samples for pups and on Corpus albicans, Feb., and Mar. -April samples for yearlings and adults

² Mean percentage based on straight combination of frequencies

³ Mean percentage based on combination of frequencies weighted by Mar. -Apr. age distribution

straight combination of age-specific ovulation frequencies each weighted by its respective sample size. This approach assumes that the population was sampled at random and hence that the age composition observed in my samples reflected that of the actual breeding population. Obviously this assumption is violated in the December collections. I will further examine this assumption in later sections.

The individual monthly samples should meet this assumption better than the "combined samples" for the following reason. A comparison of the ovulation frequencies and accompanying 90 percent confidence intervals in the February samples with the percent ovulating based on the corpus-albicans and March-April samples reveals that the percentage of pups ovulating by the time of the February collections was significantly less than the percentage of pups ultimately ovulating (Table 7). Similar comparisons among the yearling and adult age groups reveal no significant difference in ovulation frequencies between these samples. Hence pups apparently ovulate and presumably breed later than yearlings and adults. Therefore, February ovulation frequencies appear valid only for yearlings and adults and were included in the 2-3 year totals data only for these two age classes. Pup ovulation frequencies were based only on March-April and corpus-albicans samples. Consequently, the yearling and adult age classes will be over-represented to some extent in the over-all-mean-ovulation frequencies as determined by the straight-combination method.

When comparing the "overall" categories between years, it must be assumed that any collecting biases do not change. If they do, and one or more age classes are affected, the mean ovulation frequencies will not be directly comparable. Based on discussions presented later, I assume my data do not substantially violate these assumptions.

The second method of estimating overall ovulation frequencies involved weighting the ovulation frequency of each age class by its respective percentage occurrence in the March-April age distributions. Use of this method assumes the sample March-April age distribution represents the actual age distribution of the population in March and April. Separate March-April age distributions were obtained in 1973 and 1974, hence the weighting procedure in these 2 years utilized these respective age distributions. My only estimate of the 1972 March-April age distribution was obtained by combining the 1973 and 1974 distributions for that period, the same one used in weighting the 2-3 year totals. However, since the population trend was different in 1972 than in either of the succeeding years, the combined age distribution may not actually reflect the actual 1972 breeding age distribution. This approach has several added advantages. First, ovulation frequencies, as determined from winter collections obtained from a population with a different age distribution than during the previous breeding season, can be weighted by the age distribution of the previous spring. Secondly, if the sample sizes, expressed as percentages of the total sample size for all three

age classes, accumulated for each age class are not representative of the age distribution of the breeding population, the overall mean-ovulation frequency will not be affected as when using the straight-combination method since the age-specific ovulation frequencies are weighted by the March-April age distribution and not the sample size of each age class. As examples, compare the overall frequencies obtained by each method for the 1974 February samples and 2-3-year total February samples. In both cases, the weighted-mean frequencies are much higher than the straight-combination mean frequencies. In each case, the pup age class was obviously over-represented and therefore contributed more weight to the overall mean frequencies than it should have. Significantly, this sample-size problem had no effect on the overall mean frequency determined by weighting with the age distribution. However, in most cases, the overall mean frequencies were not too different between methods (Table 7).

One problem with this approach is that it is impossible to obtain a sample size for the weighted-mean ovulation frequency. This eliminates the possibility of conducting statistical tests between years. However, the standard deviation of the weighted-mean ovulation frequency can be calculated by using the standard deviation of all three constituent age classes (not shown in Table 7).

Some age-specific ovulation frequencies (2-3 year totals) were statistically different when tested by chi-square. Significantly fewer

pups ovulated than either yearlings ($\chi^2 = 3.18$, $p = 0.08$, 1df) or adults ($\chi^2 = 8.88$, $p < 0.005$, 1df). Yearling and adult ovulation frequencies were not significantly different ($\chi^2 = 0.57$, $p = 0.46$, 1df). The overall ovulation frequency ("combined samples") in 1972 was significantly less than the 1974 frequency ($\chi^2 = 3.43$, $p = 0.07$, 1df) but did not differ significantly from the 1973 frequency ($\chi^2 = 1.77$, $p = 0.20$, 1df). Similarly, ovulation frequencies did not differ significantly between 1973 and 1974 ($\chi^2 = 0.51$, $p = 0.48$, 1df).

Finally, although between-year comparisons of the weighted frequencies cannot be tested statistically, visual comparison of the mean frequency and standard deviation in each year suggests ovulation-frequency patterns similar to those discussed above. In conclusion, the 1972 ovulation frequency was probably lower than that occurring in 1973 and 1974. In addition, the data suggest that ovulation frequencies increase with age.

A major objective of this study was to estimate reproductive rates of this population. In order to accomplish this, it was necessary to measure the proportion of females pregnant and ultimately the percentage of females bearing young. Direct observation of the percentage of pregnant females in the late-winter carcass collections and percentage with placental scars in the early-winter collections provided pregnancy-rate estimates in each year.

Canids that ovulate but do not become pregnant experience pseudo-pregnancy for about 60 days; functional corpora lutea are present for about 1 month (Asdell 1946). Therefore, during the first month after ovulation, corpus structures present could be either corpora lutea of pregnancy or corpora lutea of estrus. Mansell (1971) reports a microscopic technique for distinguishing these two bodies in white-tailed deer based on appearance of corpus blood vessels. I made no attempt to make this distinction. Embryos reach the uterine horns by the 5th or 6th day, and embryonic swellings are not apparent until 14 days after ovulation and fertilization (Gier 1968). In my analysis some females in the late February collection had visible implantation sites; however, most animals which had ovulated by late February lacked definite implantation sites. Of those females with corpora lutea (indicating ovulation) but lacking visible implantation sites, a large majority had uteri which I will refer to as "zig-zag." Each uterine horn had from 2 to 5 evenly spaced areas along its length, each forming the outside of a sharp curve in the uterine horn and at each of these points there was a slight suggestion of uterine swelling. I am assuming that this zig-zag uterine condition occurs during the early stage of blastocyst implantation. If this assumption is incorrect, my estimates of pregnancy rates are too high.

My observed pregnancy rates are based on those coyotes having either implantation sites or zig-zag uterine horns, and on December placental-scar data (Table 8). Frequencies based on February

Table 8.--Percentage of Northern Utah and Southern Idaho Coyotes Pregnant, 1972-74

Breeding season	Data source	% Pregnant, 90% Conf. Int., and (Sample Size) by Age Class				Wtd. Mean % Pregnant ³ and Std. Dev.
		Pup	Yearling	Adult	Overall ²	
1972	Dec. samples	33, 9- 67 (6)	60, 25- 89 (5)	100, 46-100 (3)	57, 36- 78 (14)	70 ± 9.02
1973	Dec. samples	50, 20- 80 (6)	--	100, 50-100 (4)	70, 35- 88 (10)	--
	Feb. samples	21, 8- 42 (14)	29, 8- 68 (7)	80, 40- 98 (5)	35, 21- 54 (26)	41 ± 9.66
	Mar-Apr samples	100, 10-100 (1)	100, 62-100 (5)	100, 10-100 (1)	100, 68-100 (7)	100 ± --
	Combined samples ¹	57, 30- 83 (7)	100, 62-100 (5)	100, 62-100 (5)	82, 64- 93 (17)	88 ± 5.11
1974	Feb. samples	12, 3- 29 (17)	67, 20- 96 (3)	80, 40- 98 (5)	32, 16- 50 (25)	62 ± 11.87
	Mar-Apr samples	100, 32-100 (2)	50, 14- 86 (4)	100, 86-100 (11)	88, 71- 97 (17)	88 ± 6.25
2-3 year totals						
	Dec. samples	42, 18- 71 (12)	60, 25- 89 (5)	100, 68-100 (7)	62, 45- 78 (24)	72 ± 8.46
	Feb. samples	16, 6- 31 (31)	40, 19- 66 (10)	80, 50- 94 (10)	33, 22- 46 (51)	50 ± 7.64
	Mar-Apr samples	100, 46-100 (3)	78, 48- 94 (9)	100, 82-100 (12)	92, 78- 98 (24)	92 ± 4.86
	Combined samples	53, 32- 75 (15)	71, 42- 87 (14)	100, 87-100 (19)	77, 64- 86 (48)	78 ± 5.30

¹ Based on Dec. + Mar.-Apr. samples² Mean percentage based on straight combination of frequencies³ Mean percentage based on combination of frequencies weighted by Mar.-Apr. age distribution

collections are lower than those based on March-April and placental-scar observations (Table 8), because February is too early in the breeding season for all pregnant animals to show signs of pregnancy. Even the March-April observations may be slightly conservative for the same reason.

Placental-scar data may provide the most realistic pregnancy-rate estimates. The December collections preceded uterine development, and there was consequently no chance of missing placental scars due to uterine thickening. Resorption sites and/or 2-year-old scars were easily distinguishable from darker full-term scars. Hence, all tracts included in the placental-scar categories represented full-term pregnancies.

I used the same approach in summarizing the pregnancy-rate data as in summarizing the ovulation-frequency data. Age-specific rates and two estimates of overall rates are presented for each sample in each year. The assumptions behind these data are the same as in the previous section. The age-specific data in the combined samples (2-3 year totals) suggest that the pup pregnancy rate was significantly less than the adult rate ($\chi^2 = 8.49$, 1 df, $p < 0.005$) and that the yearling rate may have been significantly less than the adult rate ($\chi^2 = 3.79$, 1 df, $p = 0.05$). The results of the chi-square test on the annual pregnancy rates ("overall" column) suggest that pregnancy rates may not have been significantly different between years ($\chi^2 = 4.62$, 2 df, $p = 0.10$). Had the pregnancy rates weighted by the March-April age

distribution been used, there would have been even less variation between years. A comparison of straight-combination and age distribution-weighted pregnancy rates reveals relationships similar to those discussed in the ovulation-frequency section. Specifically, the December 1972 and February 1974 samples reveal this problem. As before, the pup age class was over-represented in the overall-pregnancy rates due to disproportionate sample sizes but was not over-represented when weighted with the March-April age distribution. Although most other comparisons are not as affected, the age distribution weighting method seems most realistic.

In general, the data suggest an increase in pregnancy rates in progressively older animals. Placental-scar data for all years combined imply pregnancy rates of 42, 60, 100 and 62 percent, respectively, for pups, yearlings, adults and all age classes combined during the course of my study. Combined placental-scar + March-April data imply pregnancy rates of 53, 71, 100, and 77 percent, respectively, for the same age classes.

Breeding Dates

Ten pregnant coyotes were obtained in this study which contained fetuses large enough to assess the age via techniques developed by Johns and Kennelly (unpub. data). This allowed back dating to approximate date of conception (Figure 5). The six dates for adult females suggest they conceived between late January and early February. Data from

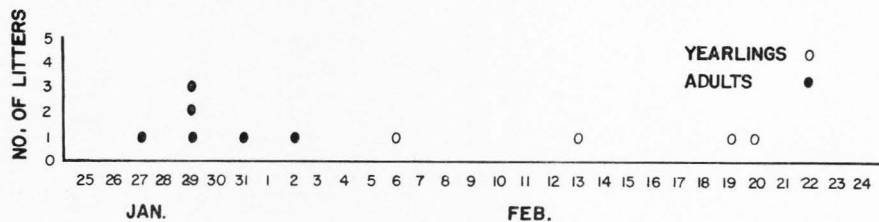


Figure 5. Conception dates estimated by aging fetuses from ten pregnant females in the winter carcass collections.

the four yearlings indicate they conceived in February. No pregnant pups were obtained, but presumably, they would have conceived later than adults, possibly even later than yearlings.

The ovulation-frequency and pregnancy-rate data support this observation. Comparison of the February ovulation-frequency and pregnancy-rate estimates with those of the combined corpus-albicans and March-April samples, and of the combined placental-scar and March-April samples, respectively, shows that a smaller percentage of the pups destined to ovulate and/or implant had done so by the time of the February samples. Similarly, a greater percentage of the yearlings and adults destined to ovulate and/or implant had done so by the time of the February collections. Hence, younger animals appear to breed later than older ones as reported for some other canid species. Alaskan wolves (Canis lupus) breeding for the first time usually enter estrus somewhat later than older females (Rausch 1967). Similarly, yearling (10 months of age) silver fox normally breed 8 to 9 days later than adults (Pearson and Basset 1946).

Litter Size

Gier (1968) concluded that careful placental-scar counts, excluding resorption and 2-year old scars, provided accurate measures of litter size. Calculated litter sizes of red fox usually fell between mean fetal and placental-scar counts (Layne and McKeon 1956).

My litter-size estimates are based on placental-scar, implantation-site, and fetal counts, all with small sample sizes. In addition, corpus-luteum counts provide maximum estimates of litter size. Sample sizes are largest in the placental-scar data because few tracts were collected late enough in the breeding season to contain implantation sites or fetuses.

Table 9 presents litter-size data for a sequence of post-ovulatory stages. Litter-size estimates generally decrease with each successive post-ovulatory stage, undoubtedly because of incomplete fertilization of all ova and intra-uterine mortality.

My best estimates of mean litter sizes were obtained by combining placental-scar counts with fetal counts. Implantation-site counts, although very close to fetal and placental-scar counts (Table 9) were not used in final estimates of litter size since early-stage resorption sites could not be distinguished from viable implantation sites in coyotes collected this early in gestation. Placental-scar and fetal-count means were not statistically different ($t = 0.54$, 40 df, $p > 0.50$).

I estimated overall mean litter sizes (overall and weighted mean columns, Table 9) by the same weighting procedures used in combining the age-specific ovulation- and pregnancy-rate data. Analysis of variance results ($F = 0.14$, $v_1 = 2$, $v_2 = 39$) suggest that there was no significant difference in mean litter sizes ("overall" column) between years at the 95 percent level. The large mean adult litter size in 1972 was due to one of the three litters in this sample having 13 pups, and

Table 9.-- Estimates of Mean Litter Sizes in Northern Utah and Southern Idaho Coyotes, 1972-74

Breeding season	Data source	Mean, 90% Conf. Int., and (Sample Size) by Age Class				Wtd. Mean ² and Std. Dev.
		Pup	Yearling	Adult	Overall ¹	
1972	Placental scars	6.2 \pm 1.21 (6)	6.2 \pm 1.50 (6)	9.0 \pm 6.07 (3)	6.7 \pm 1.04 (15)	7.3 \pm 1.63
1973	Corpora lutea	11.0 \pm 6.30 (2)	5.6 \pm 1.76 (4)	9.0 \pm 6.07 (3)	8.0 \pm 1.91 (9)	8.0 \pm 1.26
	Implantation sites	6.0 \pm -- (1)	5.7 \pm 2.58 (3)	7.0 \pm 6.30 (2)	6.2 \pm 1.09 (6)	6.1 \pm --
	Fetal counts	--	5.5 \pm 9.46 (2)	--	5.5 \pm 9.46 (2)	--
	Placental scars	5.8 \pm 0.43 (5)	5.5 \pm 15.80 (2)	6.0 \pm 1.39 (10)	5.9 \pm 0.86 (17)	5.7 \pm 1.74
	Fetal counts + placental scars	5.8 \pm 0.43 (5)	5.5 \pm 2.80 (4)	6.0 \pm 1.39 (10)	5.8 \pm 0.79 (19)	5.7 \pm 1.46
1974	Corpora lutea	7.7 \pm 3.51 (3)	5.8 \pm 1.17 (8)	6.2 \pm 0.60 (13)	6.3 \pm 0.61 (20)	6.4 \pm 0.90
	Implantation sites	--	--	7.0 \pm 4.45 (3)	7.0 \pm 4.45 (3)	--
	Fetal counts	--	6.0 \pm 6.30 (2)	6.0 \pm 1.37 (6)	6.0 \pm 1.01 (8)	--
<hr/>						
2-3 year totals	Corpora lutea	9.0 \pm 2.34 (5)	5.8 \pm 1.17 (8)	6.7 \pm 0.90 (16)	6.8 \pm 0.71 (29)	6.9 \pm 1.20
	Implantation sites	6.0 \pm -- (1)	5.7 \pm 2.58 (3)	7.0 \pm 1.91 (5)	6.4 \pm 1.08 (9)	6.3 \pm --
	Fetal counts	--	5.8 \pm 1.76 (4)	6.0 \pm 1.37 (6)	5.9 \pm 0.88 (10)	--
	Placental scars	6.0 \pm 0.60 (11)	6.0 \pm 1.39 (8)	6.7 \pm 1.42 (13)	6.3 \pm 0.65 (32)	6.3 \pm 1.40
	Fetal counts + placental scars	6.0 \pm 0.60 (11)	5.9 \pm 0.95 (12)	6.5 \pm 1.00 (19)	6.2 \pm 0.52 (42)	6.2 \pm 1.23

¹ Mean litter size based on straight combination of frequencies² Mean litter size based on combination of frequencies weighted by Mar.-Apr. age distribution

thus the mean litter size was an artifact of the small sample size.

Similarly, when analyzed by analysis of variance, the mean litter sizes in the 2-3 year totals row showed no age-specific differences at the 95 percent level ($F = 0.34, v_1 = 2, v_2 = 39$). Litter-size estimates, as determined by either combination scheme, were nearly identical. My best estimates of mean litter sizes for pups, yearlings, adults and all females combined during the course of this study are 6.0, 5.9, 6.5, and 6.2 respectively. An additional litter size estimate (6.2) is based on 12 complete litters recovered during our denning operations. Collectively, these estimates are similar to those of other studies (Hamlett 1938; Gier 1968; and Knowlton 1972).

Total Reproductive Rate

The total reproductive rate of a population may be estimated by multiplying pregnancy rates by litter sizes. By using a mean litter size (Table 9) and mean pregnancy rates (Table 8), I calculate the number of young produced per 100 females in Curlew Valley in 1972 and 1973 to have been 382 and 476, respectively, for the overall data and 511 and 501, respectively, for the weighted-mean data. Comparable estimates for 1974 could not be made because I lacked a litter-size estimate for the pup age class, although by visual inspection it appears as though productivity would have been similar to that in 1973. The importance of these reproductive rates will be discussed in a later section.

Sex Ratios

I acquired three sets of sex-ratio data during this study: sex ratios of denned pups (May), fall-trapped coyotes (September) and winter-collected coyotes (December through April). Combining the 1972 denning data (L. Charles Stoddart, Personal Communication) with that of 1973 and 1974 yielded a total sample of 81 pups. The sex ratio (males: females) of these pups (0.57:0.43) was not significantly different from a 0.50:0.50 sex ratio when tested by Chi-square ($\chi^2 = 1.50$, 1df, $p = 0.23$). To be sure there were no collecting biases involved, only those litters from which all pups were thought to be recovered were used in this tabulation. This sex ratio represents that of pups 4 to 8 weeks old; I have no data on whelping sex ratios of pups.

September trapping provided a second set of sex ratio data. The pup sex ratio of 0.39:0.61 ($n = 121$) was significantly different from the expected 0.50:0.50 sex ratio ($\chi^2 = 6.02$, 1df, $p = 0.12$). Similarly, the sex ratio of yearlings and adults combined was 0.74:0.26 ($n = 39$). This is a highly significant departure from the expected 0.50:0.50 sex ratio ($\chi^2 = 9.26$, 1df, $p < 0.005$). The overall sex ratio of 0.48:0.52 did not differ significantly from a 0.50:0.50 sex ratio ($\chi^2 = 0.40$, 1df, $p = 0.54$). It is perhaps coincidental that the overall sex ratios are as close to 0.50:0.50 as they are. Both the pup and the yearling and adult sex ratios suggest extreme sex-specific trapping biases.

Juvenile females seem more vulnerable to trapping than juvenile males; to the contrary, older females seem less susceptible than older males. An adult sex ratio this skewed is not advantageous to a monogamous species, hence there is reason to suspect these results. The fact that the trapping sex ratio of pups is bracketed on one side by the reasonable denning sex ratio and on the other side by the reasonable pup sex ratio in the winter carcass collections (to be discussed next), further invalidates the fall trapping sex ratios. I suggest that these sample sex ratios are poor estimates of the actual fall sex ratios and are a result of biases associated with trapping. Winter carcass-collection sex ratios were tabulated for both the pup, and the yearling and older age classes in both years. Chi-square tests of sex ratios in the samples for these latter two groups revealed no significant difference between years. Results for the pup age class were $\chi^2 = 0.65$ (1df, $p = 0.56$) and for the older animals were $\chi^2 = 0.03$ (1df, $p = 0.88$). Therefore, the data from both winters were combined and subdivided by months (Table 10).

Chi-square test of the pup sex ratio indicates a significant difference from a 50:50 sex ratio ($\chi^2 = 3.24$, 1df, $p = 0.07$). With a Chi-square value of 0.47 (1df, $p = 0.50$), the sex ratio of older coyotes did not differ significantly from 50:50. Therefore, the apparent excess of males in the pup age class is reduced by the time they reach yearling and older ages.

Table 10. --Sex Ratios of Coyote Populations in Curlew Valley and Vicinity, Winters of 1972-73 and 1973-74 Combined

Age class	Percent Male and (Sample Sizes) by Month				
	Dec.	Jan.	Feb.	Mar-Apr	Totals ¹
Pup	52 (60)	58 (125) ²	52 (63)	60 (10)	55 (278) ²
Yearling + older	51 (75)	52 (125)	65 (54) ³	40 (30)	52 (306)
Unknown	54 (11)	74 (27) ³	60 (5)	50 (6)	65 (51) ³
Combined	51 (146)	57 (277) ³	58 (122) ²	46 (46)	54 (635) ³

¹ Includes 44 coyotes dated only as December-January 1973-74

² Significantly different from 50:50 at 90% level

³ Significantly different from 50:50 at 95% level

In all three of the age-class categories (Table 10), the December sex ratios were not significantly different from 50:50. However, the percentage of males in the January collections was significantly greater than 50:50 in the pup and unknown age classes. Similarly, the percentage of males in the February collections was significantly greater than 50:50 in the yearling and older age class. March-April sex ratios did not differ significantly from 50:50. The percentage of males in the combined category did not differ significantly from 50 percent in the December and March-April collections, although the percentage of males was significantly greater than expected in both the January and February collections.

The picture that seems to emerge from these results is a December sex ratio near 50:50. The percentage of males in the yearling-

and-older and unknown classes increases in the January and February collections. Since this is the period of breeding onset, the increase conceivably reflects greater vulnerability of males to the sampling source perhaps because of heightened activity and movement. By March-April the percentage of males is now below the December value, perhaps because the animals are paired and settled down to denning, and because the males experienced disproportionately higher mortality than the females during the previous 2 months.

No consistent trend is evident in the pups. Whether the monthly variation in this age class is due to sampling error, or some different relationship between sampling and activity than that in the older animals, is not clear.

Age Distributions

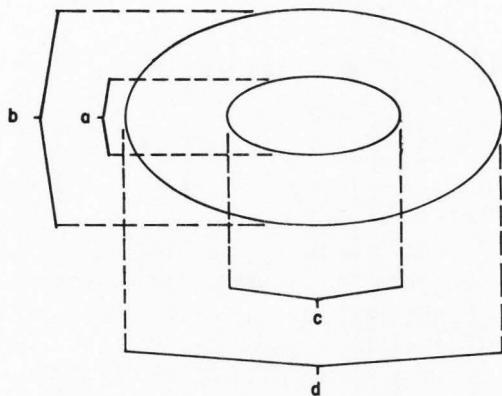
Modifications of Age Criteria

Separating pups from older coyotes: Linhart and Knowlton (1967) reported that the root tips of canine teeth in coyotes close between the 8th and 9th months of life. By identifying pups on the basis of open root tips, they were able to separate them from older animals and avoid the more tedious operation of tooth sectioning for age determination in this, the largest age class. My carcass collections began in December when pups are 8 months old. By this time the root tips are completely closed in Curlew Valley coyotes, as I did not find a

single open one in the 61 pups in my December samples. Hence, other criteria were sought to identify pups.

Linhart and Knowlton (1967) examined measurements of pulp-cavity widths and the combined widths of the dentine and cementum at the gumline. Carl Nellis (1975) developed a subjective method based on the examination of posterior-anterior canine and alveolar lengths at the gumline. My own preliminary examinations suggested that four criteria of canine teeth might provide the most complete separation of pups and older animals: (1) pulp-cavity cross-sectional lengths, (2) pulp-cavity cross-sectional widths, (3) the ratio of pulp-cavity cross-sectional length to tooth cross-sectional length, and (4) the ratio of pulp-cavity cross-sectional width to tooth cross-sectional width. Figure 6 details the way in which I obtained these measurements after separating the crown from the root at the gumline.

Linhart and Knowlton (1967) suggested that pup pulp cavities were larger than yearling pulp cavities. Pulp cavities did in fact decrease in size with age in coyotes I examined. The decreases in pulp-cavity dimensions followed a very distinct pattern proceeding from an oblong shape in pups to a circular shape in older coyotes (Figure 7). Pulp-cavity lengths varied from about 7.0 mm in pups to 0.4 mm in older coyotes, an 18-fold difference. Pulp-cavity widths varied from about 3.4 mm to 0.3 mm, an 11-fold difference. Thus, as a coyote ages, both pulp-cavity measurements become more similar, and the

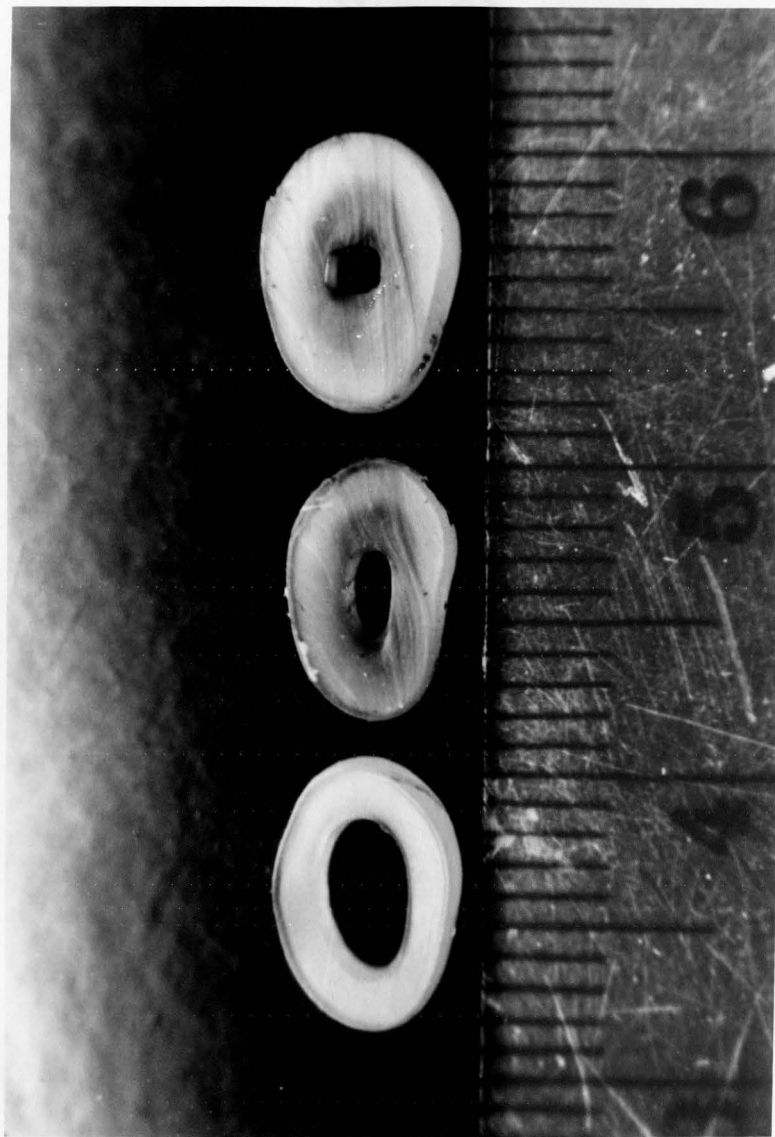


TOOTH CROSS-SECTIONAL WIDTH (b)
 PULP-CAVITY CROSS-SECTIONAL
 WIDTH (a) WIDTH RATIO = $\frac{a}{b}$

TOOTH CROSS-SECTIONAL LENGTH (d)
 PULP-CAVITY CROSS-SECTIONAL
 LENGTH (c) LENGTH RATIO = $\frac{c}{d}$

Figure 6. Measurements and ratios evaluated in pup-adult separation schemes (canine cross section at the gumline).

Figure 7. Pattern of decreasing pulp-cavity sizes as coyotes age.
Pup (left), yearling (middle), adult (right). Millimeter scale at bottom.



rate of change per unit of time must be greater for the length than the width dimension. Therefore, length measurements would presumably give a better pup-adult separation than width measurements.

I tested this assumption by plotting data from all four methods. The length-ratio plots (Figure 8) clearly gave the best separation between pups and older coyotes; hence, this was the method I used. Coyotes with length ratios of 0.32 or larger were considered pups while those with length ratios less than 0.32 required sectioning and staining to determine age. This point of separation undoubtedly changes throughout the year.

Yearling and adult age determination: Annulus formation first occurs in coyotes at about 20-23 months of age (Linhart and Knowlton 1967). My carcass collections were obtained in the winter months when yearlings were 20-22 months old and the first annulus presumably was forming. As I will discuss below, annuli may also have been forming in adults at this time.

In the majority of sections which contained one or more annuli, a wide light-staining band lay exterior to the outermost annulus (Figure 9). In those sections without annuli, a similar light-staining band bridged the space between the dentine-cementum interface and periodontal membrane. Presumably, in these sections the currently forming annulus could not be distinguished from the dark-staining periodontal membrane. However, in some coyotes, an annulus could be seen very close to the outer margin of the section (Figure 10). A thin

Figure 8. Histogram of pulp-cavity length-tooth cross-sectional length ratios.

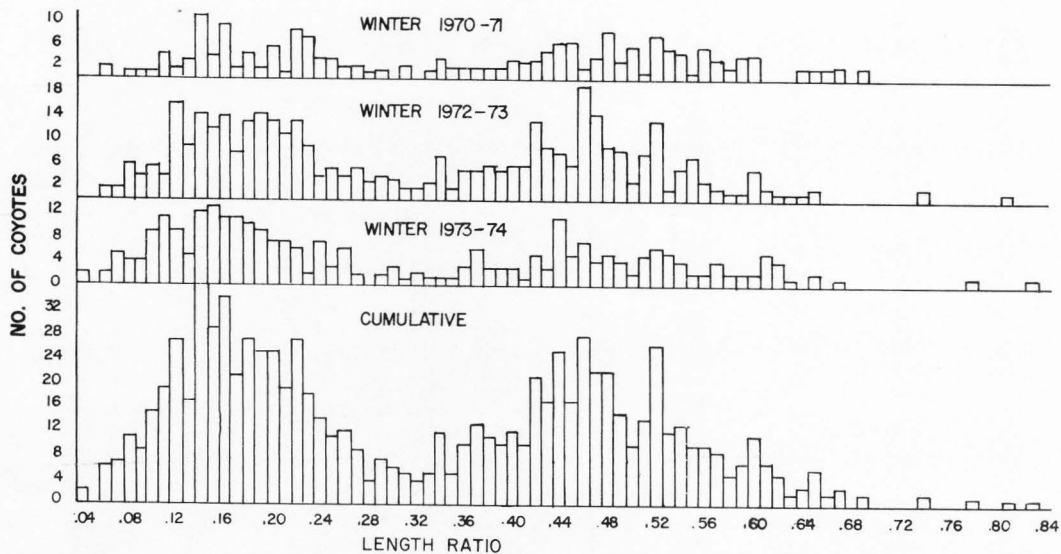


Figure 9. Canine section (67X) of a 2 1/2 year-old coyote (1 x + 1 classification and cementum measurement scheme. Tip ratio = $\frac{a}{b}$. Side ratio = $\frac{c}{d}$. Mean ratio = $\frac{\frac{a}{b} + \frac{c}{d}}{2}$. (p = periodontal membrane, i = dentine-cementum interface).

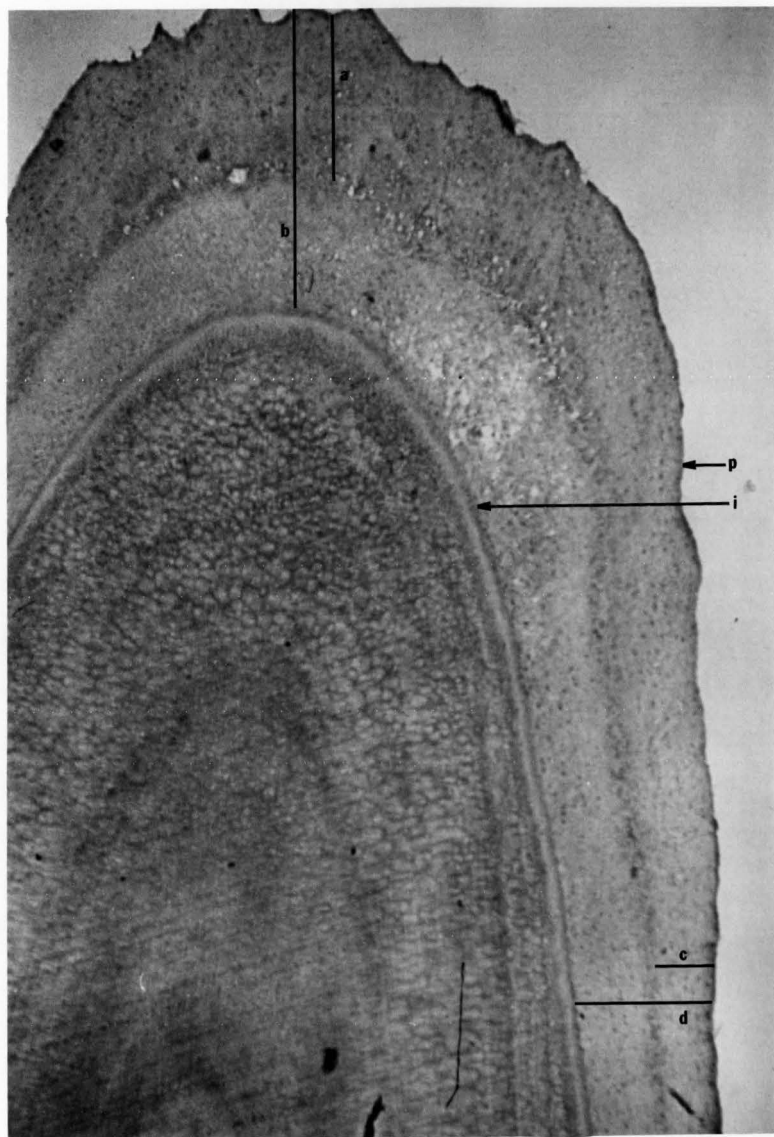
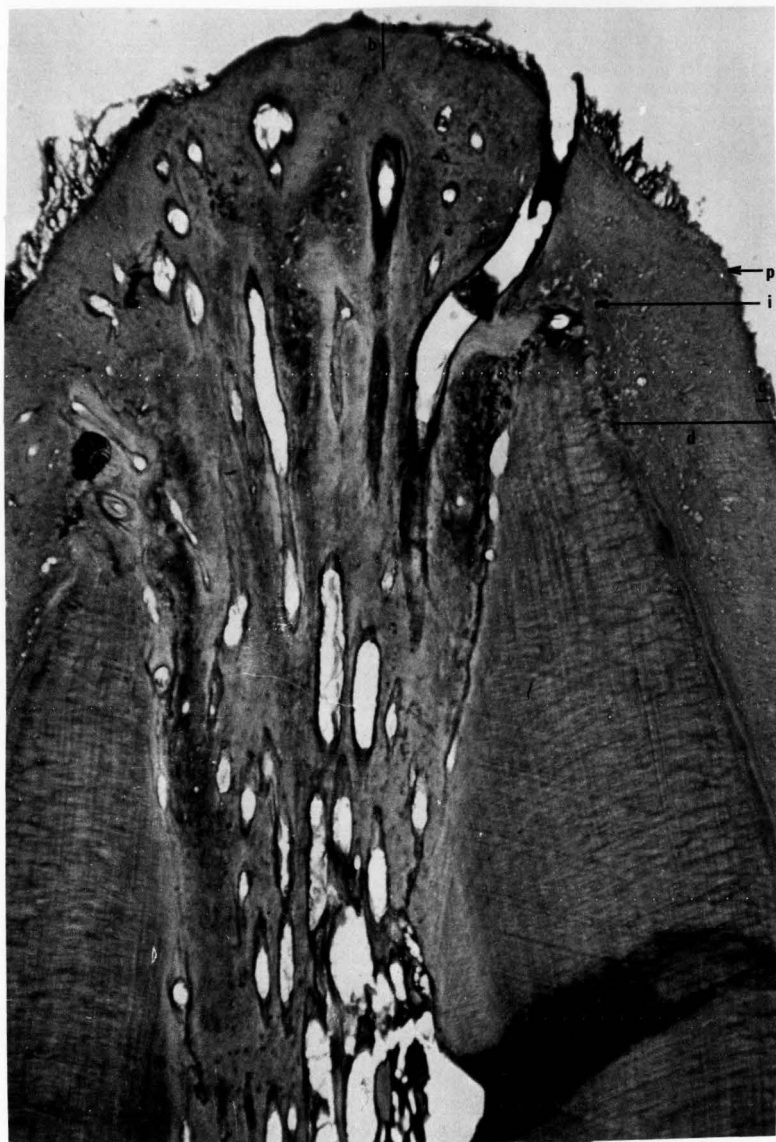


Figure 10. Canine section (67X) of a yearling coyote (1x classification) and cementum measurement scheme. Tip ratio = $\frac{a}{b}$. Side ratio = $\frac{c}{d}$. Mean ratio = $\frac{\frac{a}{b} + \frac{c}{d}}{2}$. (p = periodontal membrane, i = dentine-cementum interface).



light-staining band usually separated these annuli from the periodontal membrane. Presumably these annuli had formed during the current winter rather than the previous winter.

If my presumptions are correct in these two cases, it is possible to have two coyotes of the same age collected during a period of annulus formation with different numbers of annuli. For example, both a coyote with a single newly-formed annulus, and one lacking an annulus but having a length ratio of less than 0.32, could be yearlings. Similarly, a coyote with one annulus deep in the cementum and currently forming a second one which is still indistinguishable from the periodontal membrane, and another animal with a similar, deep-bedded annulus plus one that had just been formed and is distinguishable from the periodontal membrane would both in fact be 2.8 years of age. If this is the case, the conventional method of adding 1 year to the total number of annuli observed would in fact classify some coyotes 1 year older than their actual age.

For this reason, I separated coyotes into two groups based on the depth of their outermost annulus in the cementum. Those coyotes with a wide cementum band between their outermost annulus (presumably formed the previous winter) and the periodontal membrane were classified as " $x + 1$ " coyotes. I assume that these animals were about to form an annulus but had not yet done so. The " x " refers to the number of annuli and the "+1" indicates that 1 year is added to the annulus count

to obtain their actual age. Those coyotes with an annulus immediately inside the periodontal membrane were classified as "x" coyotes. I am assuming these coyotes had just formed an annulus. In this case, the annulus count (x) reflected their actual age and adding 1 year to the annulus count would overestimate their age by 1 year. For example, a coyote having one annulus would be classified as a yearling (1.8 years) if considered an "x" animal, or as a 2.8-year-old if considered an "x + 1" animal.

An alternative hypothesis is that there is considerable variation in the timing of annulus formation. Accordingly, the outer annuli of both "x" and "x + 1" coyotes were laid down the previous year.

I developed several cementum-measurement schemes in order to examine this problem. All measurements were taken to the nearest 0.01 mm. In those animals displaying a single annulus, measurements of the cementum thickness exterior to the annulus and the total cementum thickness between the periodontal membrane and the dentine-cementum interface were obtained (Figures 9 and 10). Measurements were taken on canine sections at the root tip and 2 mm up the sides from the root tips and on lower first premolar sections at the root tip and 1 mm up the side.

A ratio between the cementum thickness exterior to the annulus and the total cementum thickness was calculated for each coyote. A ratio was used rather than merely the cementum thickness exterior to

the annulus because there was considerable individual variation in cementum thickness and growth rates between coyotes.

For example, a coyote with 0.05 mm of cementum exterior to its annulus and a total cementum thickness of 0.10 mm would have a ratio of 0.50. Similarly, a coyote with comparable cementum thickness measurements of 0.20 mm and 0.40 mm would also have a ratio of 0.50. However, if measurements of cementum thickness exterior to the annulus alone were used, the first animal might be considered an "x" animal when compared to the second animal. Therefore, the use of a ratio should correct for variations in cementum thickness between coyotes and make the "x", "x + 1" separation more accurate.

Initially, animals for which canine tooth sections were available were placed into an "x" or "x + 1" category, based on visual inspection. I then calculated a mean ratio for each tooth section based on combined tip and side cementum ratios and plotted the frequency distributions of these ratios (Figure 11).

The results suggest a separation into two identical groups: those sections visually assigned to the "x" group all had cementum ratios of 0.20 or less; those sections visually assigned to the "x + 1" group all had cementum ratios of 0.28 or more. The clear separation held both for the 1972-73 and 1973-74 samples.

If annulus formation were occurring well in advance of, and up to, the period of carcass collection, the cementum widths between last-formed, visible annuli and periodontal membranes would seemingly vary

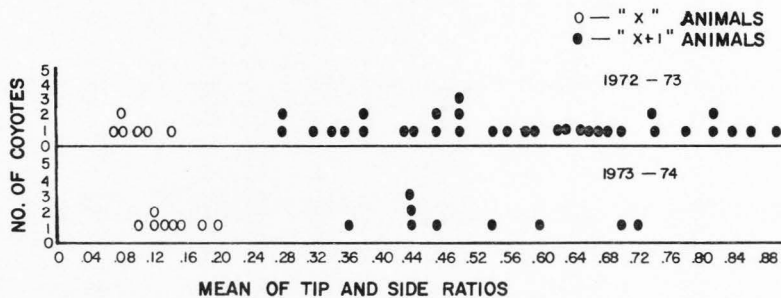


Figure 11. Mean tip and side canine cementum ratios (one-annulus coyotes).

at random over a given range. Instead they separate into two discrete ranges, which suggests that annulus formation is beginning to occur just prior to, and in, the period of carcass collection.

Figure 12 presents data similar to those of Figure 11 for coyotes aged with lower first premolar sections. These data exhibit a similar but less distinct separation between the subjectively labeled "x" and "x + 1" coyotes. This is not surprising as my data show that cementum growth rates and thickness are considerably less for lower first premolars than for canines. For example, total mean cementum thickness for canines at the tip and 2 mm up the side for "1x" coyotes (winter 1972-73) were 0.49 and 0.27, respectively, as compared to comparable lower, first-premolar means of 0.24 and 0.14. In fact, canine cementum growth rates were nearly twice that of lower first premolars in almost all age classes. Since, in the winter carcasses, annuli that I am assuming are newly formed lie close to the periodontal membrane, the cementum thickness exterior to these annuli are quite similar in both types of teeth. As previously mentioned, total cementum thickness differ by nearly a factor of two. Therefore, "x" and "x + 1" ratios should be further separated in canines than in lower first premolars because of the differences in cementum growth rates between these two types of teeth.

As previously mentioned, matching sets of canines and lower first premolars were taken from 43 coyotes. The same ages, as

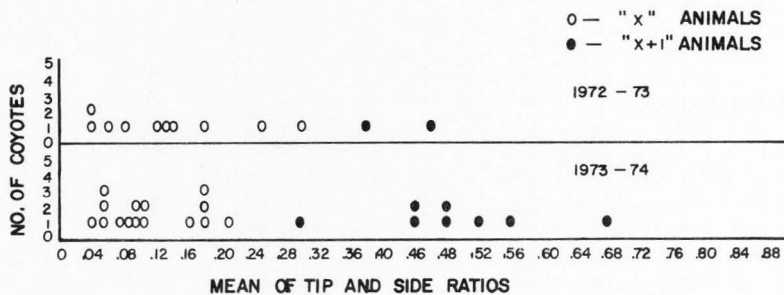


Figure 12. Mean tip and side lower first premolar cementum ratios (one-annulus coyotes).

determined by the "x", "x + 1" classification scheme, were assigned to 73 percent of the 43 animals containing one or more annuli as opposed to 59 percent agreement under the conventional aging scheme. In 27 percent of the animals, ages indicated by canines differed from ages indicated by premolars. These differences between canines and lower first premolars, as well as the apparent greater percentage of "x" animals in the lower first premolar data (Figure 12), may be due to lower cementum growth rates for premolars, different timing of annulus formation between canines and lower first premolars, or other differences between these two types of teeth. For the present, canine teeth appear to be preferable on the basis of the magnitude of separation and clarity of the annuli.

Coyotes with more than one annulus were treated somewhat differently: the cementum thickness exterior to the outermost annulus was divided by the previous year's cementum growth (inter-annulus distance, Figures 13 and 14) rather than the total cementum thickness as was done for one-annulus teeth. When these data were plotted, similar "x" and "x + 1" separations were evident.

In my experience, "x" and "x + 1" status can be assigned as accurately subjectively as it can quantitatively once a person becomes familiar with "reading" sections. This potentially eliminates the tedium of obtaining accurate cementum measurements necessary for establishing "x" and "x + 1" status.

Figure 13. Canine section (67X) of a 4 1/2 year-old coyote (3x + 1 classification) and cementum measurement scheme. Tip ratio = $\frac{a}{b}$. Side ratio = $\frac{c}{d}$. Mean ratio = $\frac{\frac{a}{b} + \frac{c}{d}}{2}$. (p = periodontal membrane,

i = dentine-cementum interface.

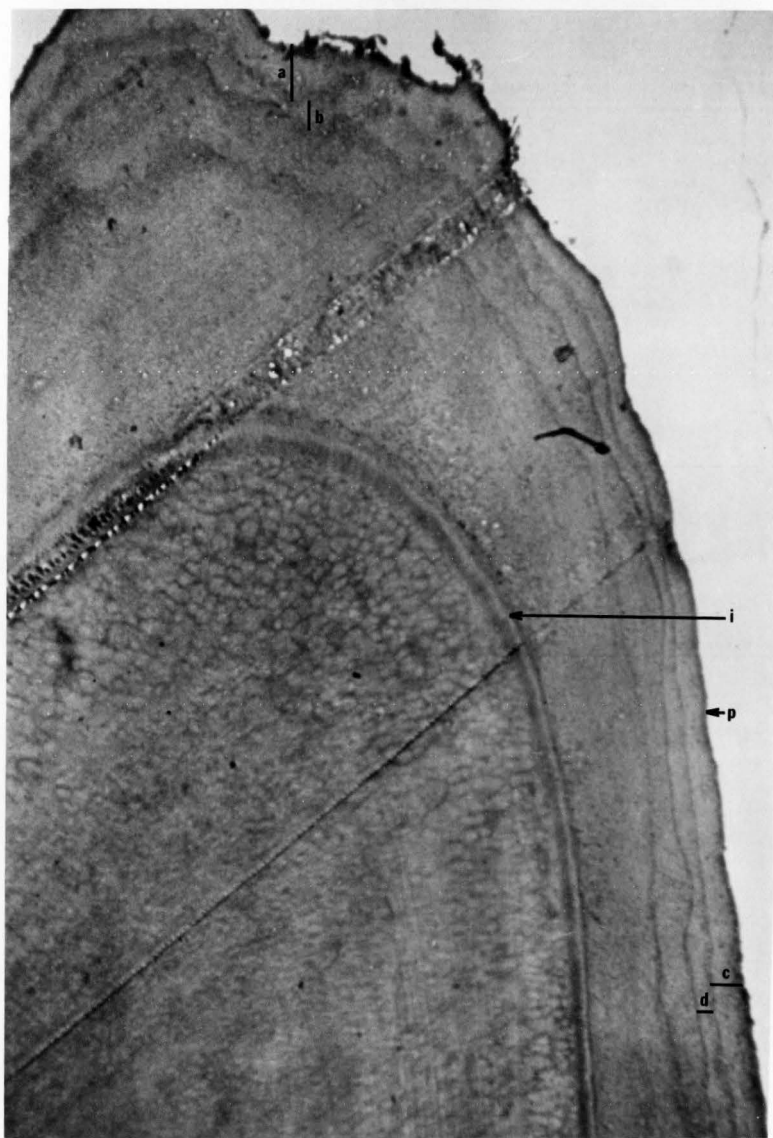
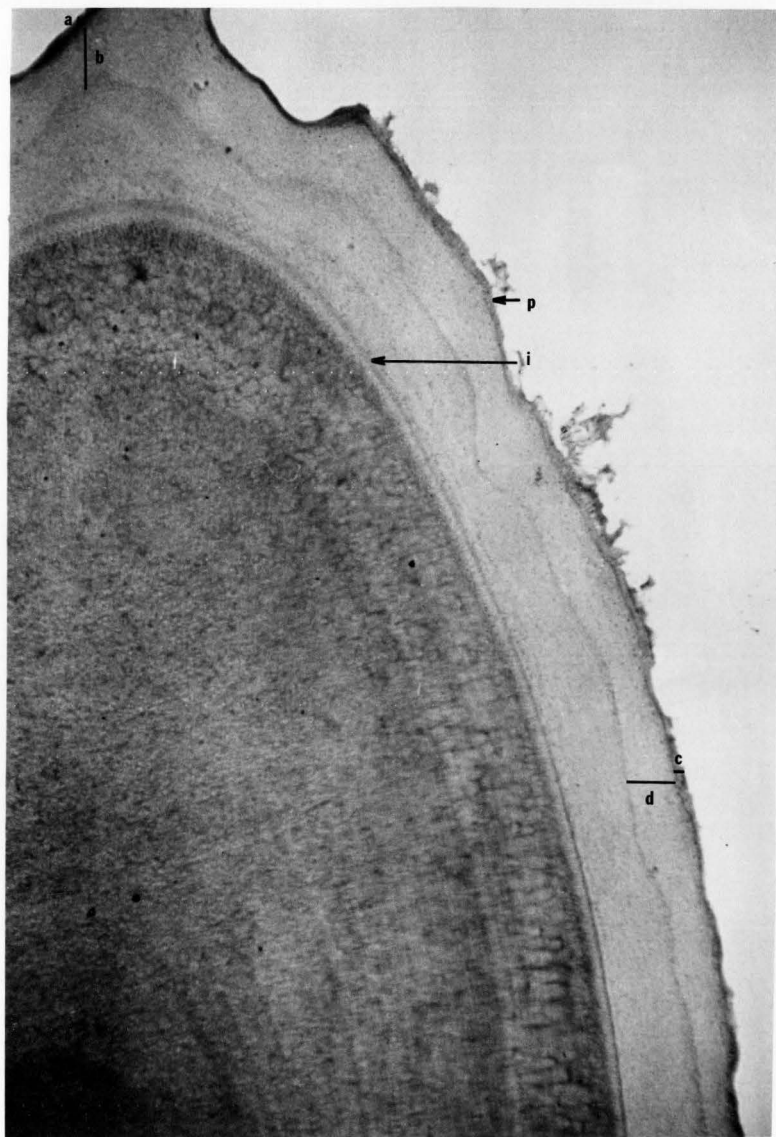


Figure 14. Canine section (67X) of a 2 1/2 year-old coyote (2 x classification) and cementum measurement scheme. Tip ratio = $\frac{a}{b}$. Side ratio = $\frac{c}{d}$. Mean ratio = $\frac{\frac{a}{b} + \frac{c}{d}}{2}$. p = periodontal membrane, i = dentine-cementum interface.



If "x" animals actually contain a newly-formed annulus, then the percentage of "x" coyotes should increase in each successive month's collections, assuming continual annulus formation throughout the winter. This increase was not obvious in my data. The percentages of "x" coyotes were 14, 46, and 18 for the months of December, January, and February, 1973-74. Similarly, no trend was observed in the 1972-73 data. Hence, either my interpretation of these results is incorrect, or the majority of currently forming annuli may not visibly separate from the periodontal membrane until sometime after late winter. Without known-aged coyotes collected from late winter through early summer, some uncertainty remains in this matter. Until this problem is resolved, animals collected during periods of annulus formation should be examined with the above classification schemes in mind.

Table 11 presents the age distributions determined by the conventional method and by the "x," "x + 1" classification schemes. There is no statistically significant difference between the age distributions as tabulated under each of these two classification schemes when tested by Chi-square in the 1970-71 and 1972-73 collections; however, the two 1973-74 age distributions may be significantly different. Results for each year are $\chi^2 = 1.56$ (4 df, $p = 0.80$), $\chi^2 = 4.30$ (5 df, $p = 0.50$) and $\chi^2 = 8.33$ (4 df, $p = 0.06$), respectively, for 1970-71, 1972-73, and 1973-74. However, the results of these statistical comparisons should not minimize the importance of making the "x," "x + 1" distinction

Table 11.--Age Distributions of Coyotes Collected in Winter in Curlew Valley and Vicinity

Age class	Percent and (No.) of Coyotes by Year and Classif. Scheme ¹					
	1970-71		1972-73		1973-74	
	Conventional ²	x, x + 1 ³	Conventional	x, x + 1	Conventional	x, x + 1
Pups	55.8 (101)	55.8 (100)	49.4 (190)	49.4 (183)	42.1 (112)	42.2 (106)
1	14.4 (26)	18.4 (33)	16.9 (65)	21.6 (80)	17.3 (46)	25.5 (64)
2	18.8 (34)	16.2 (29)	13.8 (53)	12.4 (46)	15.0 (40)	8.8 (22)
3	3.9 (7)	2.8 (5)	11.4 (44)	9.2 (34)	10.2 (27)	9.6 (24)
4	3.3 (6)	3.4 (6)	4.2 (16)	3.8 (14)	6.0 (16)	5.6 (14)
5	1.6 (3)	1.7 (3)	2.6 (10)	1.6 (6)	4.5 (12)	4.4 (11)
6	0.6 (1)	0.6 (1)	0.2 (1)	0.3 (1)	3.8 (10)	3.2 (8)
7	0 (0)	0 (0)	0.8 (3)	0.8 (3)	0.8 (2)	0.4 (1)
8	0.6 (1)	0.6 (1)	0 (0)	0 (0)	0 (0)	0 (0)
9	0.6 (1)	0 (0)	0.8 (3)	0.8 (3)	0 (0)	0 (0)
10	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
11	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
12	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
13	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
14	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
15	0.6 (1)	0.6 (1)	0 (0)	0 (0)	0.4 (1)	0.4 (1)
Totals	100.2 (181)	100.1 (179)	100.1 (385)	100.0 (370)	100.1 (266)	100.1 (251)

¹ Frequencies and totals vary between classification schemes because cementum measurements were not taken for some animals which could then not be assigned to x or x + 1.

² Ages assigned by adding 1 year to the total number of tooth annuli counted.

³ See text for method.

when animals are collected during periods of annulus formation. Conceivably, if "x" animals are a real entity, disregarding them in age distribution determination could in some cases significantly alter the age structure.

Analyses for Possible Biases

Local variations in age ratios: Of the 385 coyotes aged in the 1972-73 carcass collections, 96 percent were obtained from aerial gunning operations. Of these, only 14 percent (56 coyotes) of the entire sample were killed within the Curlew Valley study area. All animals killed outside the study area were shot to the south in three nearby areas: the Hog-up Mountains area, Park Valley area, and Bovine area. Therefore, the samples were divided into two blocks: one comprising animals taken inside the study area and one of animals from outside. Separate age distributions were tabulated according to the conventional and the "x," "x + 1" aging schemes, and Chi-square tests were used to compare the distributions between areas. The results of this test on the "x," "x + 1" distributions ($\chi^2 = 0.04$, 3 df, $p = 0.995$) suggest that these age distributions are nearly identical and therefore can be combined. Similarly, the results on the conventionally determined age distributions ($\chi^2 = 1.91$, 3 df, $p = 0.62$) suggest that these two subsamples can be combined.

In the second winter, aerial gunning operations contributed 57 percent (152 coyotes) of the coyotes aged in the sample, the remainder coming mainly from animals shot by hunters on snowmobiles. Of the aerial-gunned coyotes, 75 percent were shot outside the study area and of these about 80 percent were shot south of the study area in the same areas described above. Of the remaining 20 percent approximately 10 percent were shot immediately east of the study area between December and February. The remaining 10 percent were shot north and west of the study area in March and April. Chi-square tests of the age distributions, as determined by either classification scheme, showed no statistically significant differences between animals shot to the south and to the east of the study area, and they were combined. Results for the "x, " "x + 1" age distributions were $\chi^2 = 4.38$ (3 df, $p = 0.24$) and for the conventionally determined age distributions were $\chi^2 = 5.21$ (3 df, $p = 0.17$). I then compared the cumulative December to February age distributions of aerial-gunned coyotes from inside the study area with those from outside the study area. Results for the "x, " "x + 1" age distributions were $\chi^2 = 1.16$ (3 df, $p = 0.76$) and for the conventional age distribution were $\chi^2 = 0.09$ (3 df, $p = 0.99$). Therefore, these two samples were also combined.

All animals shot from snowmobiles were within the study area. Comparison of age distributions between aerial-gunned samples and snowmobile-hunting samples revealed no statistical difference. Results

for the "x," "x + 1" distributions were $\chi^2 = 3.42$ (3 df, $p = 0.49$) and for those conventionally determined were $\chi^2 = 2.50$ (3 df, $p = 0.62$). Hence, these two samples were also combined.

Finally, the March-April age distributions (conventional and "x," "x + 1") of coyotes aerial gunned by Wildlife Service Personnel were compared with respective cumulative December to February age distributions. The "x," "x + 1" comparisons suggest that the age distribution in March-April samples may have differed significantly from that earlier in the winter ($\chi^2 = 2.88$, 1 df, $p = 0.09$), a result to be discussed at length in the next section. To the contrary, conventional age distributions appeared to be more similar ($\chi^2 = 3.65$, 2 df, $p = 0.17$). The March-April samples were combined with the rest of the winter's data to obtain the overall 1973-74 age distribution for each classification scheme (Table 11).

Temporal variations in age ratios: I subdivided the winter carcasses according to month of collection, and calculated age ratios for each month (Table 12) in order to learn whether or not any temporal variations in behavior posed biases for age-ratio calculation.

Neither the apparent increase through February in percentage pups in either year nor the apparent March-April decline in 1972-73 is statistically real, as the 90 percent confidence intervals overlap between successive months. However, the March-April confidence intervals in the 1973-74 and totals category do not overlap with the

Table 12. -- Monthly Age Ratios of Coyotes Collected in Winter in Curlew Valley and Vicinity

Winter	Percent Pups, 90% Conf. Int., and (Sample Sizes) by Month			
	December	January	February	March-April
1972-73	42.4, 34.0-50.5 (106)	51.2, 45.0-57.0 (199)	50.0, 39.0-61.5 (64)	27.3, 10.5-58.0 (11)
1973-74	41.0, 27.5-56.0 (39)	43.6, 32.0-55.5 (55)	55.7, 44.0-67.0 (61)	25.0, 13.0-42.0 (32)
Totals	42.1, 35.0-49.0 (145)	49.6, 44.5-55.5 (254)	52.8, 45.5-61.5 (125)	25.6, 14.0-39.5 (43)

February confidence intervals, hence this decline is statistically significant. Nevertheless, this tabulation suggested a progressive increase in the samples in the percentage of pups from December through February, and then a sharp decline in March-April. Since there obviously are no young being produced at this time, some age-specific bias is evidently producing these changes. There are several possible explanations for these changes. Knowlton (1972) observed increases in the number of coyotes caught by predator-control personnel during early winter months both in areas of light and intensive predator control. However, there may have been a difference between these two areas (his Table 8, p. 376). The numbers captured per month in the lightly controlled area, expressed in terms of the percentage of the total catch, increased from September through November and declined thereafter until leveling off in March. In contrast, the numbers captured per month on the area subjected to intensive control increased from September through January and declined steadily thereafter. He postulated that the increased catch in the intensive control area resulted from ingress from peripheral areas of light control, primarily by juvenile females as suggested in his Table 9. To the contrary, the catch on the light control area was probably composed mainly of resident animals, the sex ratio of captured animals being nearly even (his Table 9).

In some respects, the northwestern corner of Utah and southern Idaho may be analogous. While both are subjected to control

by federal agents, although not to the extent of the Texas operations (Frederick Knowlton, Personal Communication), the Utah area appears to be more subject to non-governmental exploitation both because it is closer to human population centers and because Utah paid a bounty on coyotes during the period of study while Idaho did not. Consequently, the Utah area is subjected to considerable sport hunting by hunters from the cities of Logan, Tremonton, Brigham City, Ogden, and even Salt Lake City. The aerial gunners, who provided the winter carcasses, also hunted in Utah. In addition, the region is dotted with mountain ranges which are not easily hunted from the air and which have sufficient snow accumulation in winter to reduce travel. They may well receive less intensive exploitation.

In consequence, Idaho and the mountain ranges in both states may serve as foci for dispersal to the lower-altitude valleys and deserts of northwestern Utah.

Analysis of ear-tag and transmitter recovery data implies that this may have, in fact, occurred during my study. These data (Table 13) were subdivided by tagging source, age, sex and winter of recovery (first or subsequent winters). In addition, the recoveries were categorized on the basis of whether or not the coyotes involved were killed in a state other than the one in which they were initially tagged. In this analysis, I excluded animals tagged along the boundary between Idaho and Utah; the majority of the animals were tagged 5 miles or more from the boundary. Most pups and all yearlings and adults were killed in the

Table 13. --Movements (Inter-or Intra-State) of Tagged¹ Coyotes Between Initial Capture and Subsequent Recovery, 1972-1975

Tagging source and age	Sex and sample size	No. Initially Tagged and No. Recovered Inside and Outside Tagging State by Time Period							
		Recovered through end of first winter ²				Recovered in subsequent winters ²			
		U-I	I-U	U-U	I-I	U-I	I-U	U-U	I-I
Spring-tagged pups	Male (55)	0	2	6	4	0	1	0	2
	Female (38)	0	3	2	3	0	1	0	2
Fall-tagged pups	Male (44)	1	1	5	8	0	0	1	4
	Female (60)	0	6	8	9	0	0	0	3
Fall-tagged yearlings ³	Male (11)	0	0	4	2	0	0	0	0
	Female (4)	0	0	0	1	0	0	2	1
Fall-tagged adults ³	Male (14)	0	0	7	3	0	0	1	0
	Female (6)	0	0	1	0	0	0	1	0
Totals	Male & Female (232)	1	12	33	30	0	2	5	12

¹ Tagged includes ear-tagged and transmittered, ear-tagged-only, and ear-tagged and collared coyotes

² Letters U and I imply Utah and Idaho, respectively; U-I implies inter-state movement, etc.

³ Includes several coyotes transmittered in spring of 1973

same state in which they had been tagged. All but one of the 15 pups moving across state lines egressed from Idaho to Utah suggesting that movements between states were not reciprocal during this study. However, this difference may, in part, be due to greater hunting pressure and hence higher recovery rates in Utah.

Casting some uncertainty on the analogy with Knowlton's Texas areas, however, is the fact that his winter increases apparently were young females. To the contrary, the sex ratios in my collections showed an increase in the percentage of males during the winter sampling (Table 10). In addition, much of the area south of the study area is more than 30 miles (48 km) from Idaho and 10 to 15 miles (16 to 24 km) or more from the nearest mountain ranges. I am not suggesting that coyotes commonly move into these areas from Idaho or the mountains. However, much of the aerial gunning area lies along the foothills of mountains and close to the stateline, where this phenomenon could be occurring.

A second explanation suggests that the increase reflects increased movement on the part of pups within the sampled populations as the breeding season begins or as food availability decreases and established adults become increasingly intolerant. Pups may then become more vulnerable than adults and experience a higher rate of exploitation. To the contrary, the increase in the percentage of pups in 1973-74 seems to have lagged behind the 1972-73 increase (Table 12). If reproductive activity began earlier in 1973-74 than in 1972-73, and if reproductive activity has an impact on pup vulnerability, then there should

have been an earlier increase in the percentage of pups in the sample age ratio in 1973-74, than in 1972-73. I suspect this problem may be due to sampling error as only the January data conflict; the percentage of pups in the other months are quite similar.

A third possibility comes from the telemetry data (Hibler 1976). Dates on which dispersal began were obtained for six pups. These dates ranged from late September to early January and 3 of the 6 began dispersal in the latter half of November. Length of dispersal never exceeded 1 month for three pups for which initiation and termination of dispersal activities were obtained. In addition, the telemetry data showed that home range sizes of pups increased throughout the winter, although this could be an artifact of our over-winter accumulation of movement data on these animals. Thus, an increasing percentage of pups may be exposed to unfamiliar territory through dispersal and home-range expansion as the winter progresses. Presumably, pups in unfamiliar territory are more vulnerable to man's activities than are adults in the familiar territory of their established home ranges. Past experience also gives adults a decided advantage in avoiding human encounters. Similarly, dispersing red fox may be most vulnerable after cessation of dispersal when they would be establishing themselves in a new and unfamiliar area (Storm et al. 1976). This by itself, or in combination with the other possible explanations, may account for the increased pup percentages in the successive monthly sample age ratios.

Whatever the true explanation, the trends shown in Table 12 raise some question as to the true age ratios in the population at different points in time. In a later section, accurate estimates of fall age ratios will be needed to calculate annual population mortality. Both late-winter or spring age ratios, and subsequent fall or early winter ratios, will be needed to estimate postnatal pup mortality. Hence, some decision must be made on the values to be used in these estimates.

It is well known among coyote workers that pups are more vulnerable than older animals in the fall and winter. In addition, five of six pups in the movement study (Hibler 1976) began dispersal activities by December which probably increased their vulnerability. Therefore, I conclude that December sample age ratios are also biased towards pups, although perhaps to a lesser extent than in January and February. I will discuss the possible biases of December age ratios further in the next section and will conclude that December age ratios are my best estimates of fall age ratios.

The winter increase in the sample age ratios changes abruptly in March-April when pup values for those months fall below the December ratios (Table 12). Knowlton (1972) observed a similar end-of-winter decline in his south Texas samples, with reduction starting in February and continuing in March. Some decision needs to be made as to whether such a decline might actually be taking place in the population.

Late winter declines in pup-adult ratios are plausible if (1) the December sample ratios correspond reasonably well to population ratios, and (2) the overwinter mortality rate of pups is higher than that of yearlings and older animals. If these two conditions hold, age ratios should decline between December and March, and the low March-April sample ratios could approximate the population values. Two lines of evidence lend some support to this reasoning.

First the first-year mortality appears higher than that for yearlings and older animals. I have not calculated life tables and survivorship curves in the mortality section below from the data in Table 11 because the population is not stationary and the age distributions are not stable. However, some insight into the approximate magnitudes of the rates for pups and older animals can be obtained here in order to test assumption (2) above. First-year mortality rates (a_1) can be approximated by:

$$a_1 = \frac{N_o - N_1}{N_o} \quad \text{where}$$

N_o = the number of pups in the age sample

N_1 = the number of yearlings in the sample

The mean, annual mortality rate for the yearlings and older animals

(a_a) can be approximated by:

$$a_a = \frac{N_1}{N_{n-o}} \quad \text{where}$$

N_1 = the number of yearlings in the age sample

N_{n-0} = the number of animals in the age sample minus the
number of pups

For the distributions aged by the conventional method, the first-year mortality rates estimated by these procedures are .74, .66, and .59 for the three successive years in Table 12; the yearling-and-older rates respectively are .32, .33, and .30. For the distributions aged by the "x, " "x + 1" method, the respective first-year rates are .67, .56, .40, the yearling-and-older rates are .42, .43, and .44. In five out of six comparisons, therefore, the first-year rates are substantially higher than the rates for the yearling and older animals. Even if some allowance is made for the bias toward pups now under discussion, the differences remain. I do not regard these as valid estimates of the mortality rates because, as stated above, the population is not stationary. But I do tentatively infer that the first-year mortality rates are higher than those of yearlings and older animals.

Analysis of transmitter-recovery data provides additional evidence on age-specific coyote vulnerability. Of the three sources of recovery data available (ear tag, collar, and transmitter) only the transmitter data were used since mortality was most detectable by this approach. For example, mortality of ear-tagged and collared coyotes such as handling mortality (post-trapping), natural mortality, and some man-induced mortality such as failure to successfully recover fatally

wounded animals could easily go unnoticed. In addition, only two adult coyotes were ear tagged during this study.

The recoveries have been subdivided into two groups: recoveries occurring between September and December and between September and the end of the first winter (Table 14). The recovery rate of pups is based entirely on the first-winter recovery rate of fall-transmitted pups. In addition to the first-year recovery rate of fall-transmitted yearlings and adults, pups (e. g., transmitted in fall 1972) surviving to the second fall (e.g., fall 1973) and recovered as yearlings during their second winter of life (e.g., winter 1973-74) were treated as first-year recoveries of yearlings and added to the yearling and adult group. This manipulation increased the sample sizes of potentially recoverable yearling and adult males and females from 17 to 27 and 7 to 16, respectively. The 90 percent confidence intervals overlap between all four age-and sex-specific groups; hence, in the September-to-December category, no significant difference in recovery rates can be demonstrated. Nevertheless, there is some suggestion that older females may have a lower recovery rate than older males. Similarly, all age-and sex-specific confidence intervals overlap in the September-to-end-of first-winter category. Mean recovery rates (not shown in Table 14) of pups and older coyotes are 55.8 and 39.5 percent, respectively. Confidence intervals around these two percentages also overlap. However, these rates may reflect a difference in vulnerability. As in the

Table 14. --Age-Specific Coyote Vulnerability as Reflected by Transmitter Recovery Rates (Winters 1972-73 and 1973-74 Combined).

Age, sex	No trans- mitted	% Recovered During Time Interval and (90% Conf. Int.)	
		Sept-Dec.	Sept-End First Winter
Pup Male	20	25.0 (12.6-42.2)	50.0 (32.5-67.5)
Pup Female	23	26.1 (11.1-43.1)	60.9 (43.1-77.2)
Yearling and adult male	27 ¹	22.2 (9.4-36.5)	44.4 (29.1-63.5)
Yearling and adult female	16 ¹	12.5 (3.4-30.5)	31.2 (14.7-55.0)

¹ See text for explanation of sample size

previous comparison, adult females appear to have a lower recovery rate than adult males although the difference does not appear to be great and in fact may be an artifact of the small samples. This conclusion is supported by the fact that the overall winter sex ratio (winters combined) of yearlings and adults in the carcass collections was .52: .48 (Table 10), a departure that is not significantly different from a 50:50 sex ratio. Although the initial sample sizes of trans-mitted coyotes and subsequent recoveries were small, this analysis suggests that pups may indeed be more vulnerable during their first winter of life than yearlings and adults.

The second line of evidence is the seasonal distribution of mortality to be discussed below. More than 90 percent of the annual

mortality appears to have occurred between October and February during my years of study, with 67 percent occurring in the 3 winter months. Since mortality appears heavier among pups than yearlings and older animals, and since most of it seems to be concentrated in the winter months, some reduction in percentage of pups between the beginning and end of winter could logically be expected. This is consistent with the above suggestion that the January-February age-ratio increase is a function of the increased vulnerability of the pups at this time which sustain a disproportionate share of the concentrated winter mortality. Gier (1968) postulated similar explanations for year-end declines in age ratios of Kansas coyotes.

Age-specific biases in sampling: The effects of pup vulnerability and differential mortality are perhaps somewhat compensatory. Disproportionate fall pup mortality reduces the actual pup percentage in the population by December, hence the percentage of pups in a December population underestimates the percentage of pups in the fall population. On the other hand, due to pup vulnerability, the percentage of pups in the December sample age ratio probably overestimates the percentage of pups in the actual population in December. Therefore, the presumed reduction in percentage of pups by December is offset to some extent by the overestimation in the December sample age ratio. The extent to which these two processes are compensatory is unknown, but the compensation may improve the accuracy of fall age ratio estimates based on December-sample age ratios.

I have elected not to use the September-trapping data for any inferences about age composition for several reasons. First, discussions with Wildlife Services personnel and private trappers lead to the conclusion that pups are more vulnerable to trapping efforts than are adults. This is especially true in an area like Curlew Valley that has been subjected to trapping for extensive periods of time.

Secondly, the trapping sex ratios, previously described, reveal several biases in the fall-trapping data. The departures from expected 50:50 sex ratios of both pup and older age groups suggest that trapping sex ratios are subject to various sex-specific biases. If trapping-sex ratios are this biased, then trapping-age ratios might also be non-representative of actual population age ratios since there may be a greater difference in trapping vulnerability between inexperienced pups and older coyotes than between males and females of any age group. The percentage of pups in the fall trapping samples were higher than respective percentages in the December carcass collections each year: 76 and 72 percent (samples of 75 and 43) respectively for 1972 and 1973 trapping compared with 42.4 and 41.0 in the December carcass collections (Table 12).

Similarly, trapping results in a wolf study in Minnesota (Van Ballenberghe et al. 1975) strongly suggested the existence of age-specific trapping biases. Since adults learned to avoid traps after their initial capture, Van Ballenberghe, et al. concluded that trapping age

ratios may not accurately reflect actual population age ratios in heavily trapped wolf populations.

One final consideration concerns the potential age-ratio changes between early fall and December resulting from disproportionate pup mortality during this period. In a later section I will suggest that 28 percent of the annual mortality of coyotes 5 months old and older occurs between September and the end of November. I will also calculate annual mortality rates of 82 and 42 percent in 1972-73 and 1973-74 respectively. Combining the pre-December rate with respective annual mortality rates gives corrected pre-December mortality rates of 23 and 11 percent, respectively, in 1972 and 1973. I placed an upper limit on this effect by assuming that the pre-December (1972) mortality rate (23 percent) was concentrated entirely in the pup age class.

I will first assume that the fall population consists of 75 percent pups as an approximation to the trapping results. After absorbing a 23 percent loss the pup percentage in the age ratio would be reduced to 70 percent; a 7 percent reduction in the pup percentage. This reduced pup percentage is still considerably higher than the December percentage; hence the percentage of pups in the September trapping age ratio could not have been reduced to that of the December sample during this period. On the other hand, to arrive at a pup percentage of 42 percent in December after a pup loss of 23 percent, a fall population composed of 48 percent pups would be required, a percentage considerably less than that of the trapping age ratio. These two hypothetical

situations are based on an extremely unlikely situation since older coyotes undoubtedly suffer some of the September to December mortality, as previously described in the transmitter recovery rate discussion. Therefore, there would be even less change in age ratios between September and December. In the second year the September-to-December mortality rate was half that of the first year. Thus age ratios should have been less affected in the second year than in the first.

Therefore, during my study, September-December mortality did not appear to alter fall age ratios significantly by the time of the December samples. Although the December age ratios are undoubtedly biased to an unknown extent, they probably are better estimates of fall age ratios than are the trapping age ratios and are therefore my best estimates of fall age ratios. I will arbitrarily vary the December age ratios in the Discussion section to establish ranges which hopefully enclose the actual birth-to-fall pup mortality rates.

Using the December sample age ratios as estimates of the year-end (fall) population age ratios and the March-April sample age ratio as estimates of the whelping population age composition assumes that the age classes are sampled randomly in these months by the aerial gunning. The December samples obviously violate this assumption

but I have nevertheless assumed that the sample age ratio reasonably approximates the actual population age ratio. I will now examine this assumption with respect to the March-April aerial gunning samples.

One possible test would be to compare the percentage of pups in the March-April collections with the percentage of yearlings in that portion of the sample comprised of yearlings and older animals. This comparison assumes that yearlings and older animals are sampled at random, and if the March-April pup percentage were similar to the yearling percentage, it would be one indication that pups are not being sampled disproportionately.

The yearling percentages are in fact the adult mortality rates cited above, and for the conventional aging method were .33 and .30 (or 33 and 30 percent) for the 1972-73 and 1973-74 collections. For the "x" and "x + 1" aging methods, they were 43 and 44 percent. These compare with 27 percent and 25 percent pups, respectively, in the March-April samples (Table 12). The magnitudes are quite similar in the case of the conventional aging method, and in the "x" and "x + 1" case, the percentage of pups is actually lower. There is, accordingly, no suggestion in this comparison that the March-April samples are biased toward pups. To the contrary, these data suggest an over-representation of adults in these samples. But since the age compositions are changing between years, the comparisons are crude.

In addition, those pups surviving the winter are probably more aware of man's activities by March and April, and are probably less vulnerable than they were in December, and perhaps are no more vulnerable than yearlings and adults. To whatever extent one winter's experience assists a pup in coping with man's activities by March and April, this should comparably reduce the sampling biases introduced by age-specific vulnerability.

Age Composition of Curlew Valley Coyotes

The percentage of pups at the beginning of winter in 1972-73 and 1973-74 were approximately 42 and 41 percent, respectively. By March-April, my Utah percentages had declined to somewhere near 25 percent in the surviving portion of the population now about to produce young.

These percentages will be used in later sections to calculate total number of young produced, the mortality of those young between birth and fall, and the fall-to-fall mortality of the entire population.

Population Density

Relative Population Trends

Population estimates of low-density carnivore populations are invariably based on small sample sizes. Hence, I used several methods (Clark 1972) to obtain independent indices from which means, and

variances could be obtained. Five indices were used to produce a composite, fall index as follows:

Spring denning index: The denning data provide an index of spring population density, (Table 15) and are expressed as dens-per-flying-hour. In fact, this statistic is only an index to the number of dens in early May, and therefore an index to the pup population. It is an index to the total May population only to the extent that the May age ratios are relatively constant from one year to the next.

I also assume that the denning index can be used as an index to the subsequent fall population, and add it to the other fall indices. Validity of this assumption requires that pup and adult mortality rates between denning and fall trapping are the same between years.

Table 15. --Calculated Spring Denning Indices for the Curlew Valley Study Area, 1972-74

Year	No. Dens Found	No. Hours Flown	Dens-Per Flying Hour
1972	12	18.0	0.67
1973	2	18.3	0.11
1974	2	20.0	0.10

Fall trapping indices: Data from the fall trapping efforts provide indices of fall densities. Each of the three traplines served as one index, thus the fall trapping provided three density estimates. Table 16 presents the calculated index values which are based on coyotes-caught-per-1000-trap-nights.

Table 16. --Calculated Fall Trapping Indices for the Curlew Valley Study Area, 1972-74

Year	Utah Trapline			Juniper Trapline			Holbrook Trapline		
	No. Coyotes Trapped	No. Trap ¹ Nights	Coyotes-per- 1000-Trap Nights	No. Coyotes Trapped	No. Trap ¹ Nights	Coyotes-per- 1000-Trap Nights	No. Coyotes Trapped	No. Trap ¹ Nights	Coyotes-per- 1000-Trap Nights
1972	23	1446.5	15.90	26	1409.5	18.45	16	1359.0	11.77
1973	7	1467.5	4.77	9	1439.5	6.25	11	1424.0	7.72
1974	9	1419.0	6.34	8	1442.5	5.54	25	1371.0	18.23

¹ 1500 trap nights minus the number of trap nights lost due to inoperable traps (e.g. snapped traps, jackrabbit captures, etc.)

Fall scat index: The scat collections provided another fall density index, expressed as scats per week, for the Utah portion of the Curlew Valley study area (Table 17).

Table 17. --Calculated Fall Scat Indices for the Curlew Valley Study Area, 1972-74

Year	No. Scats Collected	No. Weeks of Accumulation	Scats-Per Week
1972	169	4.0	42.45
1973	75	4.14	18.12
1974	87	4.0	21.80

Composite index: Since the indices are of several kinds they need to be scaled to some common base before they can be combined to give the composite (mean) index values and associated variances. To accomplish this, I arbitrarily set the 1972 denning value equal to 100 and adjusted the other denning values (Table 18) with respect to the base 1972 value by applying the following formula:

$$x_i = \frac{X_i}{X_1} \times 100 \text{ where}$$

$$x_i = \text{adjusted denning value}$$

Table 18.--Relative and Composite Index Values, With Associated Standard Deviations and 95 Percent Confidence Intervals, for the Curlew Valley Study Area Coyote Population, 1972-1974

Relative Indices								
Year	Index Value	Denning	Utah Trapline	Juniper Trapline	Holbrook Trapline	Scat Line	Composite Index ³	95% Conf. Int. ⁴
1972	Unadjusted ¹	0.67	15.90	18.45	11.77	42.25		
	Adjusted ²	100	77	80	41	68	73+21.46	46-100
1973	Unadjusted ¹	0.11	4.77	6.25	7.72	18.12		
	Adjusted ²	16	23	27	27	29.	24+5.18	18-30
1974	Unadjusted ¹	0.10	6.34	5.54	18.23	21.80		
	Adjusted ²	15	31	24	63	35	34+18.10	12-56
Unadjusted Totals		0.88	27.01	30.24	37.72	82.17		

¹ See tables 15, 16, 17

² See text for description of conversion techniques

³ Mean of the five constituent indices \pm 1 standard deviation

⁴ $\bar{x} \pm t_{0.05} s/\sqrt{n}$

X_i = unadjusted denning value

X_1 = unadjusted 1972 denning value

100 = adjusted 1972 denning value

The other four indices were scaled to the denning index using two relationships. The relationship between the denning index and each of the other indices was established by (1) summing the three unadjusted index values for each of the five indices and (2) by dividing the sum of the denning index values by each of the sums of the other four indices. This, in effect, calculated the ratio of scat-line index and each trapping index to the denning index for the 3-year period, 1972-74.

The second relationship involves the ratio between the adjusted and unadjusted 1972 denning indices. Conversion of each of the individual yearly values for the four indices (Table 18) was achieved by the following general equation suggested by L. Charles Stoddart (Personal Communication):

$$y_i = \frac{\sum X_i}{\sum Y_i} \times Y_i \times \frac{100}{X_1} \text{ where}$$

y_i = adjusted index value for any of the four other indices

$\sum X_i$ = sum of the three unadjusted denning index values

$\sum Y_i$ = sum of the three unadjusted index values for any of the four other indices

Y_i = unadjusted index value for any of the four other indices

X_i = unadjusted 1972 denning index value

100 = adjusted 1972 denning index value

The terms $\frac{\sum X_i}{\sum Y_i} \times Y_i$ adjust the unadjusted index values to the unadjusted denning values and the ratio $\frac{100}{X_1}$ scales each index value to the adjusted 1972 denning value.

The adjusted denning index values (Figure 15) decrease each year, with the 1974 value only slightly less than the 1973 value.

Similarly, all three adjusted trap-line values decreased between 1972 and 1973 (Figure 16). However, in contrast to the denning data, index values for two of the three lines increased between 1973 and 1974. The Juniper trapline values decreased only slightly as one less coyote was caught in 1974 than 1973 (Table 16). Similarly, only two more coyotes were caught on the Utah line in 1974 than in 1973 (Table 16). Of the three traplines, the Holbrook line is the only one that registered substantially different catches between these 2 years. In fact, the catch more than doubled in 1974 (Table 16). Throughout this study the Holbrook line has differed in degree of change between years. In addition it differed in trend from that of the Juniper trapline and the denning index between 1973 and 1974.

Although the fall scat line provides data for only the Utah portion of the study area, the trends (Figure 17) are very similar to those observed in the trapping data and close to those of the denning data.

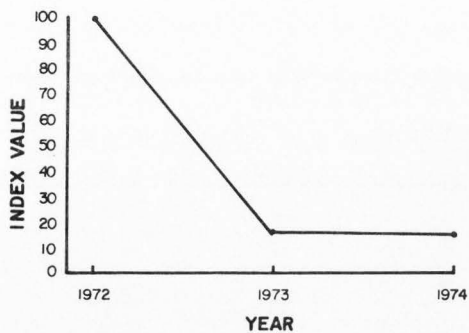


Figure 15. Relative denning indices.

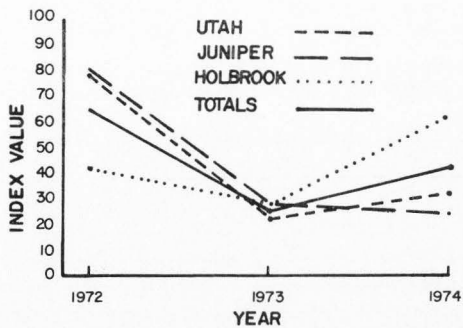


Figure 16. Relative trapping indices for the three individual traplines and the combined trapline.

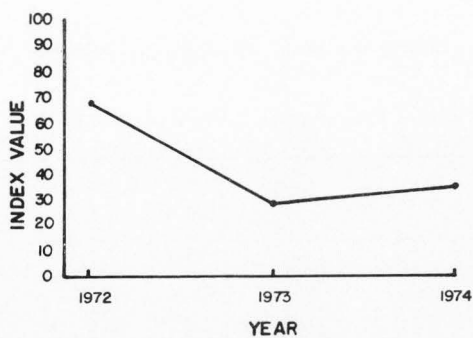


Figure 17. Relative scat-line indices.

The trends in the composite index plot (Figure 18) are, as is to be expected, similar to the trends of its constituent indices. The mean or composite index value is my best estimate of the relative population density for any particular year because it is based on an average of five indices and, therefore, should not be as subject to sampling error as a single index method. Since, in some cases, the confidence intervals overlap (Figure 18), I cannot say that the population density, as reflected by the composite index, differed significantly between 1973 and 1974 or 1972 and 1974. Nevertheless, my best estimates of the population trends for the study area as a whole suggested that the population decreased from high densities in 1972 to considerably lower densities by 1973. By 1974, the density may have increased slightly.

The spring index (denning) and fall indices (trapping and scat line) reflected similar trends between 1972 and 1973. Hence, the trend for the remainder of the year might be set by the time the pups reach the age at which they are subject to our denning activities. However, with the exception of the Juniper trapline, these trends did not agree between 1973 and 1974. Either the relationship between spring and fall densities is not a constant one, or else the discrepancy is due to sampling error. With only two dens found each spring in 1973 and 1974, the latter alternative would seem likely.

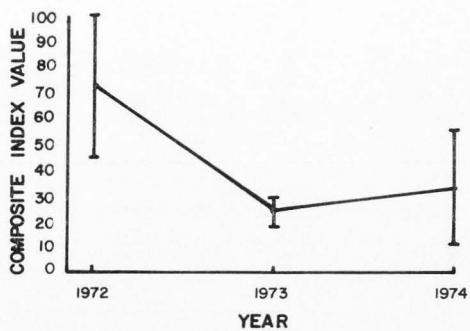


Figure 18. Composite relative index values and accompanying 95 percent confidence intervals.

Absolute Density Estimates

Assumptions: Five assumptions must hold if capture-recapture density estimates are to be unbiased. I will now consider these in sequence and examine the evidence for their validity.

In a spatial sense, either the marking procedure (denning) or the recapture procedure (trapping), or both, must be randomly distributed. The study area was flown as thoroughly as possible during the allotted 20 hours. Aerial searches were conducted randomly in all areas except the roughest mountain and foothill canyons where, because of the danger involved, searches were not made. Much of the Idaho portion of the study area is covered by juniper forest and sagebrush. The sagebrush in Idaho is often larger than that occurring in Utah. Hence, dens were probably more observable in the Utah portion of the study area than in the Idaho portion. Nevertheless, the denning index is still valid since observability of dens in the various vegetation types should not have varied between years.

I have previously described the procedure Clark used in locating the three traplines. Since most of the study area is accessible by road, the traplines covered all types of terrain including the mountains. They did cover some areas in which denning efforts could not be conducted.

A second assumption is that similar mortality rates exist between tagged and untagged pups from the time of initial capture to the time of subsequent recapture efforts. During my study (springs of 1973 and 1974) all dens were visited a day or two after the tagging operation to look for mortality among tagged pups. In every case the dens were vacated and no dead pups were found. These efforts would detect neither predation on the pups nor mortality that occurred away from the den. Although I have no way of evaluating the extent of these potential mortality factors, I am assuming they are minimal.

Additional evidence for minimal post-tagging pup mortality comes from an analysis of spring-tagged pup returns. Of the 16 dens of pups tagged during the three springs of 1972-74, pups from 15 were subsequently recovered by various means through the end of winter 1974-75, and two or more animals were recovered from 11 of the 16 litters. Of the 95 pups tagged, 40 percent (38) have been recovered as of this writing.

First-year (late-fall and winter) recovery rates and total recovery rates (cumulative recoveries from all three winters) of spring-tagged and fall-tagged pups provide another means of evaluating this assumption. For the sake of this comparison, only those pups that were ear tagged during the fall trapping session were used. Thus ear-tagged-only coyotes (as opposed to ear-tagged and transmittered animals) were involved in these comparisons. Similar recovery rates

for these two groups would imply that minimal post-tagging mortality of spring-tagged pups had occurred: i.e. all spring-tagged pups had survived up to the time of the fall trapping efforts. If, on the other hand, spring-tagged pup recovery rates were lower, post-tagging mortality of spring-tagged pups would have occurred. These data would not be sufficient to determine whether or not the spring-tagged pups suffered a different mortality rate than untagged pups between the time of spring tagging and fall trapping, but would merely indicate that some pup mortality or loss of tags had occurred during the summer. Tag loss was apparently minimal. If some percentage of spring-tagged pups lose both ear tags, a greater percentage probably lose only one. Since only 8 percent ($n = 12$) of the recovered spring-tagged pups had lost one ear tag during this period, a smaller percentage lost both ear tags.

The first-year recovery rate and 90 percent confidence interval (parenthetical) for spring-tagged pups of 23.8 percent (16-32, $n = 84$) compares with a fall-tagged pup recovery rate and confidence interval of 32.2 percent (18-49, $n = 31$). Hence some post-tagging mortality of spring-tagged pups may have occurred although this difference cannot be shown statistically. To the contrary, total recovery rates and 90 percent confidence intervals of 31 percent (22-41, $n = 84$) and 35.5 percent (22-52, $n = 31$) for spring-tagged and fall-tagged pups respectively suggest minimal post-tagging mortality of spring-tagged pups, although

once again these differences are not significant. By comparing the two recovery rates it is possible to estimate the extent of spring-tagged pup loss. The total recovery rates were used because of the larger recovery samples and longer lengths of time in which recoveries were documented. Using these two rates an over-summer, spring-tagged pup loss of 12.7 percent ($\frac{35.5 - 31.0}{35.5} \times 100$) is indicated.

In summary, some post-tagging pup mortality probably occurs. The significant question is whether or not the mortality rates of the spring-tagged and untagged pups differ. I suggest that the time following our denning activities may be the crucial period determining whether or not the female accepts the pups we have handled. Once she accepts them presumably their chances of survival are equal to that of untagged pups. All my data suggest that females do accept these litters. I am assuming that spring-tagged pups survive as well as untagged pups. However, if the trauma of handling makes the tagged pups more susceptible to mortality factors than untagged pups, the effect would be to reduce the tagged-to-untagged ratio and would produce a bias toward over-estimation of the May pup population.

A third assumption that must be made is equal susceptibility of both tagged and untagged pups to recapture. Pups were tagged at 5 to 6 weeks of age and were about 5 months old in September. Nothing is known about how handling these pups affects their susceptibility to subsequent recapture efforts. But since they were tagged 4 months prior

to the recapture efforts, and since the recapture techniques differed substantially from the initial capture techniques, this effect may have been negligible or nonexistent. However, if the spring-tagged pups displayed more caution or greater trap avoidance than untagged pups, the fall untagged-to-tagged ratio would be too high and the population overestimated. On the other hand, the population would be underestimated if there is a trapping bias in favor of the spring-tagged pups.

The final two assumptions deal with rates of ingress and egress between spring denning and fall trapping activities. Telemetry data on the dates of the initiation of dispersal activities were obtained for six pups (Hibler 1976). One pup began dispersing in late September, another began in October, three began in November and a sixth started in early January. Hence, some slight dispersal activities begin as early as September; however, most of it occurs well after the end of the September trapping efforts. In Texas, significant numbers of coyotes begin dispersing in November; dispersal activities apparently increase through January and decrease thereafter (Knowlton 1972). Red fox in the Midwest disperse as early as late September, but the majority disperse during October (Storm et al. 1976).

Additional data on the extent of pup movement between denning and fall trapping were obtained by calculating the mean distance between den and trap site locations for those spring-tagged pups that were also

caught during the subsequent fall trapping session. This value was compared with two additional values: mean distance between den and subsequent first-winter recovery locations for spring-tagged pups; and mean distance between fall trap site and subsequent first-winter recovery locations for fall-tagged pups. The mean denning-to-fall-trap-site distance (2.0 miles, 3.2 km) was significantly less than both the mean denning-to-winter recovery distance (5.5 miles, 8.8 km) ($t = 2.96$, 32 df) and mean fall trap site-to-winter recovery distance (7.5 miles, 12.1 km) ($t = 2.78$, 41 df) at the 99 percent level. Collectively, these data suggest that dispersal activities of most pups do not begin until sometime after the September trapping. If this assumption is violated, the untagged-to-tagged ratio would be unaffected by egress as long as both tagged and untagged animals disperse at the same rate. But ingress would add to the number of untagged animals and increase the ratio. The result would be an overestimation of the May population.

A critical review of the above assumptions suggest that the estimates are potentially susceptible to several biases. All of those considered, if present, would produce overestimation of population size. In my judgment, none of these operated significantly. Nevertheless my capture-recapture estimates should be considered as maximum density estimates.

Absolute density estimates: The capture-recapture data accumulated during this project provided pup density estimates for three

springs (1972-1974) (Table 19) using Bailey's (1952) adjusted Lincoln Index formula for small sample sizes. Total spring population densities were obtained by dividing the pup density estimates by their respective percent pup values in the December age ratios. As previously mentioned, the December age ratios are my best estimates of May age ratios. Since some summer pup mortality occurs, the December pup percentages will underestimate the actual May pup percentages resulting in overestimation of the total May population densities. To correct for this, I reconstructed what the pup percentage may have been in May based on the December age ratio and the May-to-September pup mortality-rate estimate of 13 percent.

The small number of tagged pup recaptures resulted in large standard deviations and extremely wide confidence intervals around the pup population estimates. Standard deviations around the 1973 and 1974 estimates overlap as do the 1972 and 1974 deviations (Figure 19). Similarly, the 95 percent confidence intervals overlap for all 3 years (Table 19).

Total spring population estimates (Figure 20) follow the same pattern as the spring pup estimates. These estimates are probably bracketed by even wider standard deviations and confidence intervals since additional error was introduced by using the pup percentages (F in Table 19). Although changes in density cannot be statistically shown, the fact that the population estimates follow the same trend as

Table 19. --Estimated Numbers of Coyotes in the Curlew Valley Study Area in May, 1972-1974

Year	No. pups marked in May (a)	No. pups caught in September (n)	No. marked caught in September (r)	Estimated No. pups in May (p) ¹	One standard deviation (S) ²	95% confidence intervals ³	Estimated % pups in May population F = $\frac{\% \text{ pups in Dec.}}{.87}$ ⁴	Total May population (T = P/F)	Coyotes/ Mile ² in May (T/700)
1972	70	51	6	520	171	214-1385	49	1061	1.5 (0.6) ⁶
1973	11	19	2	73	34	16-590	47	155	0.2 (0.1)
1974	14	33	1	238	133	33-9004	68 ⁵	350	0.5 (0.2)
Totals and means	95	103	9	831	--	--	--	522	0.7 (0.3)

$$^1 p = \frac{a(n+1)}{r+1}$$

$$^2 S = \sqrt{\frac{a^2(n+1)(n-r)}{(r+1)^2(r+2)}}$$

³ Calculated from Chapmans (1948) 95% confidence interval table

⁴ Table 12

⁵ Approximated from a cursory examination of carcasses (n = 29) collected after expiration of this project

⁶ Coyotes/km² (T/1813 km²)

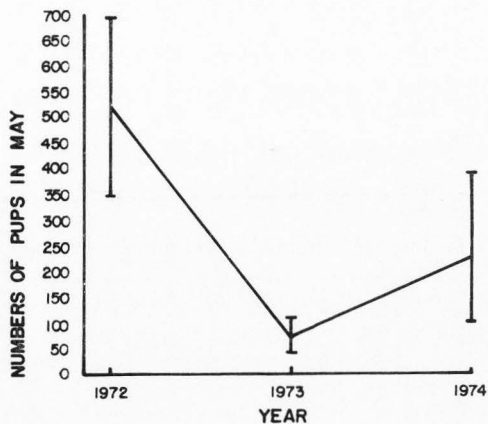


Figure 19. Capture-recapture May pup population estimates. Brackets represent one standard deviation.

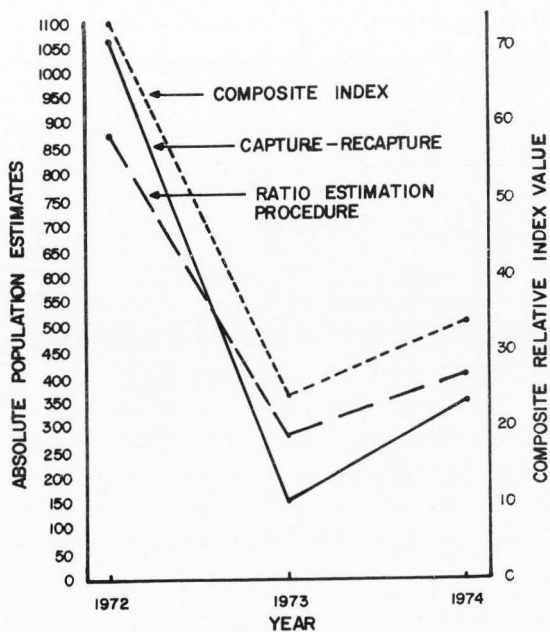


Figure 20. Comparison of the two sets of absolute density estimates with the composite relative index values.

the composite relative index values, give mutual support to the validity of both (Figure 20).

The 95 percent confidence intervals for the composite index values are narrower than those of the absolute density estimates suggesting that more confidence can be placed in the former. Therefore, an alternative approach to absolute density estimation involves multiplying the individual composite index values by the ratio between the pooled absolute density estimates and the pooled composite relative index values. In other words, the average relationship between the absolute density estimates and the composite index values is used to estimate absolute densities based on the less variable individual composite index values (Table 20). The trends of the new density estimates not surprisingly parallel those of the composite index values. These estimates

Table 20. --Estimated Number of Coyotes in May (1972-74) in the Curlew Valley Study Area Based on the Relationship Between the Pooled Composite Index Values and the Pooled Absolute Density Estimates

Year	Composite Index (a)	Mark-Recapture Density Estimates (b)	Ratio Density Estimates ($\Sigma b / \Sigma a \times a$)
1972	73	1061	873
1973	24	155	287
1974	34	350	406
Totals and Means	131	1566	522

are, of course, still affected by the original biases present in both sets of values used for establishing this ratio.

Since the composite index appears to reflect population trends more accurately than the capture-recapture estimates, as reflected by the narrower confidence intervals, perhaps the density estimates based on the composite index are more realistic. These two sets of estimates agree rather closely except for the 1973 values which differ by nearly a factor of two. Thus, the capture-recapture estimates suggest maximum May densities ranging from 0.2 to 1.5 coyotes per square mile (0.1 to 0.6 coyotes per km^2) and the other set of density estimates suggest a range varying from 0.4 to 1.2 per square mile (0.2 to 0.5 coyotes per km^2).

The percentage of dens found as well as the percentage of pups trapped during the study can be estimated. Of the 104 pups trapped during the 3 years, 9 were marked suggesting that one den in 11 was found. Similarly, 104 of the estimated 831 pups, at the time of our denning efforts, were trapped during the three September trapping periods. This suggests that one pup in eight was caught by the trapping efforts. Since some pup mortality probably occurred between denning and September, more than 1/8 of the pups were caught, depending on the magnitude of mortality.

Mortality

Annual Fall-to-Fall Population Mortality

Mortality-rate estimates: Annual fall-to-fall mortality rates of the entire population can be calculated by comparing the total population size in the fall of 1 year with the number of yearlings and older animals in the fall of the following year. I made these calculations by comparing the composite index value (Table 18) of 1 year with the product of the index value of the following year and the fraction of yearlings and adults in the carcass collections of the latter year (Table 12). Mortality rates, expressed as percentages, are estimated by:

$$m = \frac{I_t - (I_{t+1} \times a_{t+1})}{I_t} \times 100 \text{ where}$$

m = annual, fall-to-fall percent mortality

I = composite index value for year t or $t + 1$ (Table 18)

a = fraction of yearlings and adults in December of year
 $t + 1$ (Table 12)

Aside from the assumptions made in the case of the composite index and age ratios described above, the major assumption involved in using this equation is that there is no differential movement into or out of the study area. Since the study area is surrounded on all sides

by coyote range, any substantial degree of movement into or out of it would presumably be reciprocal.

My data allow mortality-rate estimates for 2 years (Table 21): 1972-73 and 1973-74. The rate for the second year (42 percent) was half that of the first (82 percent).

Table 21.--Procedure for Estimating Fall-to-Fall Population Mortality Rates for Curlew Valley Coyotes, 1972-73 and 1973-74

Year	Composite index ¹ (I)	% Adults in Dec. ² (a)	No. Adults in index (I x a)	% Mortality $\left(\frac{I_t - (I_{t+1} \times a)}{I_t} \times 100 \right)$
1972	73	58	--	--
1973	24	59	14	82
1974	34	41 ³	14	42

¹ From Table 18

² From Table 12

³ From a cursory examination of 29 carcasses collected after expiration of this project

Although my ear-tag and transmitter recovery rates cannot be used to estimate annual mortality rates directly, they can serve as an index to mortality rates. Neither the first-winter transmitter recovery rates (90 percent confidence intervals are parenthetical) of 52 percent (40-64, n = 48) and 58 percent (39-72, n = 19), nor those of ear-tagged-only coyotes of 18 percent (8-34, n = 22) and 54 percent (30-80, n = 11)

for 1972-73 and 1973-74, respectively, showed the same between-year trends as the census and age-ratio mortality-rate estimates. Transmitter recovery rates were equivalent to 63 and 152 percent of the estimated mortality rates in these 2 years. Ear-tag recovery rates were 22 and 142 percent of the estimated mortality rates in the same years.

Some discussion seems in order concerning the observed discrepancies in trend between the tag and/or transmitter recovery rates and the census and age ratio mortality-rate estimates. As previously mentioned, the transmitter-recovery data are more reliable than the ear-tag data because a greater percentage of mortality can be detected with transmitters. Nevertheless, I will first consider the ear-tag results. The 90 percent confidence intervals overlap; hence, these ear-tag recovery rates are not significantly different. The small number of ear-tagged animals released during this study may have contributed substantially to this wide discrepancy between years.

I will discuss sources of mortality in the next section but will not subdivide it by years. Therefore, I will now briefly discuss annual sources of mortality as it may explain the differences in ear-tag recovery rates between years. At least 6 and probably 9 of the 25 transmitted coyotes recovered in winter 1972-73 were aerial gunned whereas only one of the 11 transmitted coyotes recovered in winter 1973-74 was aerial gunned. None of four, and one of five, ear-tagged coyotes

recovered were aerial gunned in winters 1972-73 and 1973-74 respectively. Significantly, eight of 11 transmitter recoveries and three of five ear-tag recoveries in 1973-74 were made by snowmobilers. These data, when coupled with interviews with the aerial gunners themselves, suggest that greater numbers of coyotes were killed by aerial gunning operations in 1972-73 than in 1973-74.

Apparently, the aerial gunners could easily distinguish transmittered coyotes from the air and recovered them whenever they shot one. To the contrary, ear-tagged-only coyotes were usually not recognizable from the air. Additionally, the aerial gunners indicated that in winter 1972-73 they were able to recover only about half of all coyotes shot, hence some ear-tagged-only coyotes may have been shot but not recovered. The lower ear-tag recovery rates in 1972-73 may have been due to the high percentage of animals killed by the aerial gunners in that winter, whereas the increased recovery rates in 1973-74 reflected the reduction of aerial gunning pressures and increase in other hunting pressures, particularly snowmobile hunting.

The similarity of transmitter-return rates between years is also surprising in light of the substantial changes in estimated annual mortality rates between these years. Several possible explanations for these results exist. First, the coyote study and its objectives were probably familiar to more people by the second year of the study. If so, even if a smaller percentage of coyotes were killed in the second

year, as indicated by the estimated mortality rates, a higher percentage of tags and transmitters may have been turned into us, even though our return address was on each ear tag and transmitter both years.

A second and more probable explanation involves hunting intensity between years. Transmitter-recovery data and discussions with aerial gunners indicate that fewer coyotes were killed by this method in 1973-74 than in 1972-73. In fact, aerial gunning pressure was probably also reduced in 1973-74. On the other hand, transmitter recoveries indicate a substantial increase in snowmobile kills in 1973-74 (from 0 to 8). In addition, while conducting weekly sessions of fieldwork and making carcass collections both winters, I noticed a substantial increase in hunting pressure, particularly snowmobiling, on the study area in the second winter. Perhaps the snowmobile kill compensated for the reduced aerial gunning kill on the study area during the second winter.

Thus far this discussion has only considered mortality rates, as evidenced by transmitter recoveries, on the study area. There was probably less hunting pressure over the vast areas south of the study area (Figure 1) from which many of the carcasses were obtained than in the study area, particularly in the second winter as suggested by two lines of evidence. First, much of this area is less accessible than most parts of the study area; hence, aerial gunning probably constitutes

a greater percentage of the hunting pressure in these areas. Secondly, since the aerial gunning operations were reduced in intensity the second winter, hunting pressure on coyotes south of the study area may have even been less. On the study area the increase in snowmobile hunting compensated in part for the reduction in aerial gunning. Therefore, it could be possible to have lower mortality rates over the area as a whole (shaded area in Figure 1) but yet have similar transmitter-recovery rates on the study area between years. Whatever the true explanation(s), I assume that the census and age-ratio estimates of mortality rates more reliably estimate the mortality parameters for the coyote population in the 700 mi² study area than the ear-tag and transmitter-recovery rates.

Sources of mortality: Tagging and telemetry data provided evidence on the causes of coyote mortality in Curlew Valley. The telemetry aspect of this study was intended to detect natural and any other mortality which otherwise might be missed by relying solely on ear-tag returns.

Clark (1972) reported that during his years of study, virtually all detected coyote mortality in Curlew Valley was man-induced. Similarly, all of my ear-tag returns were from human causes, specifically coyote hunting (Table 22).

Telemetry data (Table 22) are nearly identical with those of the ear-tag data. Of the 52 transmitter returns, 98 percent were

Table 22. --Causes of Coyote Mortality in Curlew Valley Based on Ear Tag, Transmitter, and Collar¹
Recoveries from Coyotes that were Trapped and Released During the Three Falls 1972-74 and May 1973.
Recoveries Have Been Recorded Through Winter 1974-75

Cause of Death	% and (No.) Recoveries by Marking Method			
	Ear tag ²	Transmitter ²	Collar ²	Transmitter ³
Hunting coyotes	100.0 (10)	67.3 (35)	66.7 (10)	60.0 (6)
Snowmobile	40.0 (4)	23.1 (12)	20.0 (3)	10.0 (1)
Aerial gunned	10.0 (1)	17.3 (9)	13.3 (2)	30.0 (3)
Shotgun ⁴	--	5.8 (3)	13.3 (2)	--
Calling	--	7.8 (4)	20.0 (3)	10.0 (1)
Other means	50.0 (5)	13.5 (7)	--	10.0 (1)
Incidental to other activities	--	7.8 (4)	6.7 (1)	10.0 (1)
Duck hunting	--	1.9 (1)	6.7 (1)	--
Mountain lion hunting	--	1.9 (1)	--	--
Deer hunting	--	1.9 (1)	--	10.0 (1)
Unspecified	--	1.9 (1)	--	--
Trapping	--	1.9 (1)	26.7 (4)	--
Unknown recoveries	--	5.8 (3)	--	--
Shot by small caliber rifle	--	1.9 (1)	--	--
Scavenged (possibly shot)	--	1.9 (1)	--	--
Unknown	--	1.9 (1)	--	--
Road kill	--	1.9 (1)	--	--
Natural mortality	--	1.9 (1)	--	--
Staphylococcic pneumonia	--	1.9 (1)	--	--
Handling oriented ⁵	--	13.5 (7)	--	30.0 (3)
Total No. Recoveries	100.0 (10)	100.1 (52)	100.1 (15)	100.0 (10)

¹ Coyotes in fall 1974 were eartagged and fitted with collars (not transmitters)

² Trapped and released in fall

³ Trapped and released in spring

⁴ These coyotes were probably shot from the air

⁵ These coyotes were probably shot from the air

man-induced mortalities. The single case of documented natural mortality involved a female pup that apparently died from staphylococcic pneumonia in late February, 1974.

Coyote hunting activities accounted for 67 percent of the transmitter recoveries. Hunting coyotes from snowmobiles has increased in popularity during the past few years and accounted for 23 percent (all in 1973-74) of the transmitter returns. Each winter local sheep ranchers and, to a lesser extent, Division of Wildlife Services personnel, shoot coyotes from planes. This activity has accounted for 17 percent of the transmitters recovered. In addition, I recovered three transmittered coyotes in the field that had been shot with shotguns, presumably from aircraft, as all three contained BB shot which is the load most often used by the aerial gunners. If this is the case, then snowmobiling and aerial gunning accounted for the same number of returns; combined, 46 percent of the returns came from these sources. Four transmittered coyotes (8 percent) were killed by hunters using predator calls. The "other means" category (Table 22), including hunting techniques such as road hunting, accounted for 14 percent of the recoveries.

Coyotes are shot each year incidental to other activities such as big and small game hunting. This category accounted for 4 (8 percent) of the transmitter recoveries. Although several people trap on the study area, only one transmittered coyote was recovered by this method. Miscellaneous recoveries accounted for the rest of the returns.

The handling-oriented category includes those coyotes that were recovered in the field shortly after release. Deaths were attributed to the effects of trapping and handling and as such should not be considered a normal source of mortality.

The discussion above deals only with coyotes caught and released during the 1972 and 1973 fall trapping sessions. Collar recovery data (Table 22) for coyotes caught and released during fall 1974 are very similar to the results of the ear-tag and transmitter recovery data. Transmitter recoveries (Table 22) of coyotes trapped and released in May 1973 also follow similar patterns.

Natural mortality would be under-represented if some animals died in locations not conducive to signal transmission or carried malfunctioning transmitters. Several instances were observed in the field where transmitted animals emitted a much-reduced signal intensity when in holes or drainage ditches, even though reception distances were only 1 or 2 miles (1.6 to 3.2 km). This increases the possibility that some natural or even man-induced mortality went unnoticed; however, frequent monitoring flights and the location of permanent receiving stations on top of mountains and foothills decreased the chances of undetected mortality. Furthermore, recovery rates constitute a very large fraction of the estimated mortality rates leaving little room for natural mortality of any magnitude.

In total, 25 of the 87 coyotes transmittered during this project are unaccounted for. The fates of these coyotes are unknown and should not be attributed entirely to natural mortality. Several cases of transmitter malfunction occurred during the study which accounts for some of the missing animals. Most recovered transmitters were mutilated (by biting) to various degrees. If, in the process, the acrylic cases were punctured or cracked allowing moisture to enter, malfunctions likely occurred. In addition, some of these coyotes are probably still alive and should be recovered in the future. In fact, several animals were still transmitting at the termination of the study. In conclusion, I am assuming that few transmittered coyotes died without being detected and that if any did, knowledge of their fates would not appreciably alter the results.

Collectively during my study, nearly all of the mortality of coyotes 5 months or older in Curlew Valley was apparently man-induced. In a later section I will consider pup mortality between birth and fall. This is the age group which is probably most affected by natural mortality factors.

Timing of mortality: Assumption of little or no yearling and adult mortality between spring and fall will be necessary in order to estimate birth-to-fall pup mortality rates. I tested the validity of this assumption by analyzing the kill dates of all ear-tagged-only and transmittered coyotes during the course of this study (Table 23). Nearly all

Table 23. --Monthly Distribution of Deaths Among Ear-Tagged and Transmitted Curlew Valley Coyotes, 1972-74¹

Month of death	No. of Deaths by Original Tagging Source				Percent of total
	Spring tagging	Spring trapping	Fall trapping	Combined totals	
January	10	3	18	31	29
February	5	1	13	19	18
March	0	0	0	0	0
April	0	0	1	1	1
May	0	0	0	0	0
June	0	0	3	3	3
July	0	1	0	1	1
August	0	0	0	0	0
September	0	0	1	1	1
October	2	2	8	12	11
November	4	0	13	17	16
December	8	0	13	21	20
Totals	29	7	70	106	100

¹ These returns include both ear-tagged-only and transmitted coyotes

mortality of yearling and adult coyotes occurs between fall and spring.

In fact, 94 percent (100 of 106) of the animals were killed between October and February; the other six recoveries occurred between April and September. Similarly, Storm et al. (1976) reported that 83 percent of the documented red fox mortality occurred between October and February. This period coincides with the period of most intense hunting and trapping pressure.

In addition, of 13 transmitted coyotes monitored during the summer of 1973, 11 were recovered or monitored sometime after that summer. Of the other two animals, one was shot in July and we lost

contact with the other one in June. Therefore, I conclude that spring-to-fall mortality of yearlings and adults is minimal.

Birth-to-Fall Pup Mortality

Mortality-rate estimates: The reproductive rates calculated above can be used to calculate age ratios at birth. These ratios can be compared with fall or early winter age ratios, and the mortality rate of pups between spring and fall calculated. The mortality rate, expressed as a percentage, is calculated as follows:

$$m = \frac{\frac{P_b}{1} - \frac{P_f}{1}}{\frac{P_b}{1}} \times 100 \text{ where}$$

m = percent mortality

$P_b/1$ = number of pups per older coyote at whelping

$P_f/1$ = number of pups per older coyote in December (from

Table 12)

Aside from assuming that my reproductive-rate, age-composition, and sex-ratio calculations accurately estimate the population parameters, the major assumption underlying the use of this method is that there is no mortality of yearlings and adults between spring and fall based on the tagging and telemetry data discussed in the previous section. If this assumption is violated, and some spring-to-fall yearling

and adult mortality does occur, the estimated birth-to-fall pup mortality rates will be conservative.

My reproductive data are too few to calculate a rate for each year of my study. Consequently, I must use the mean pregnancy rates (Table 8) and the mean litter sizes (Table 9) for the mortality-rate calculations in both 1973 and 1974 (Table 24). Similarly, I used the combined March-April age distribution because of the small samples each year. Since I have assumed no yearling and adult-mortality over summer, the December sex ratio could perhaps be used to approximate the March-April sex ratio. In addition, the December sex ratio (1972 and 1973 combined) is based on larger samples than the March-April sex ratio; hence, it may be a better estimate of pre-whelping sex ratios. Since the December sex ratios do not differ significantly from 50:50, this is the sex ratio I used in these calculations. In fact, the fall age ratios are the only data subdivided by years in these calculations. Unfortunately, the use of mean values reduces the sensitivity of pup mortality rate comparisons between years.

I estimated the numbers of pups, yearlings, and adults present in a hypothetical, pre-whelping population of 100 coyotes by using the March-April age distribution. I then multiplied the total number of coyotes in each age group by the percent females in the appropriate sex ratio (Table 10) to obtain the number of females present in such a pre-whelping population of 100 coyotes. The number of females in each age group was multiplied by its respective age-specific pregnancy rate

Table 24. -- Procedure for Estimating Birth-to-fall Pup Mortality rates in Curlew Valley, Summers 1973 and 1974.

Year	Age	No. / 100 coyotes ¹ (a)	% ♀ / ♂ in December sex ratio ² (b)	No. ♀ / 100 coyotes (c = a x b)	Age-specific pregnancy rates ³ (d)	Age-specific mean litter sizes ⁴ (e)	No. pups produced/ 100 coyotes (f = c x d x e)	Whelping age ratios (g = f/100) (h = $\frac{\% \text{ pups}}{\% \text{ yrlings} + \text{older}}$)	Dec. age ratio	Est % birth-to-fall pup mort. ($-\frac{g-h}{g} \times 100$)
1973	Pup	24.4	0.50	12	0.53	6.0	38			
	Yearling	35.2	0.50	18	0.71	5.9	75			
	Adult	40.4	0.50	20	1.00	6.5	130			
	Totals	100.0					243	2.43:1	0.69:1 ⁵	72
1974	Pup	24.4	0.50	12	0.53	6.0	38			
	Yearling	35.2	0.50	18	0.71	5.9	75			
	Adult	40.4	0.50	20	1.00	6.5	130			
	Totals	100.0					243	2.43:1	1.44:1 ⁶	41

¹ Based on March-April age distribution not presented in text

² December sex ratios not significantly different from 50:50 (Table 10)

³ Table 8

⁴ Table 9

⁵ Table 12

⁶ Obtained from an analysis of carcasses (n = 29) collected after expiration of this project

(Table 8) and litter size (Table 9) to yield the number of pups produced by each age group and in total per 100 breeding coyotes.

The estimated birth-to-fall mortality rates of pups (Table 24) for 1973 and 1974 were 72 and 41 percent respectively. I assume these are estimates of over-summer pup mortality rates. If, however, the December age ratios differ from the fall age ratios, the mortality-rate estimates would apply to that period between birth and December. In addition, by combining estimated birth-to-fall and May-to-fall pup mortality rates, it is possible to determine birth-to-May pup mortality rates. I calculate these rates to be 68 and 32 percent in 1973 and 1974 respectively.

Similar calculations using the March-April sex ratios yield birth-to-fall pup mortality rates of 75 and 48 percent and birth-to-May pup mortality rates of 71 and 40 percent respectively, in 1973 and 1974. Although the magnitudes changed somewhat, the trends between years remained similar. Thus, the birth-to-fall mortality rates probably were within the range of 72 to 75 percent and 41 to 48 percent in 1973 and 1974, respectively.

DISCUSSION

Techniques Review and Evaluation

Natality

A species' demography is influenced in part by changes in age-specific pregnancy rates, litter size, and the sex and age ratios of the breeding population. It is important to obtain estimates of these parameters at the proper times. A difference in the timing of collections of only 2 or 3 weeks can make a significant difference in the reliability of these estimates, as is particularly evident in my pregnancy-rate estimates.

I estimated pregnancy rates by direct observation of pregnancies or placental scars in the carcass collections. Combining my estimated conception dates (Figure 5) with Gier's (1968) statement that embryonic swellings are not evident until 14 days after ovulation and fertilization suggests that samples collected earlier than mid-March would likely underestimate pregnancy rates, especially those of younger animals. Hence, collections after mid-March provide the most accurate pregnancy-rate estimates. In addition, December placental-scar data accurately reflect pregnancy rates.

Pregnancy rates could seemingly be estimated in another way. If reliable data on ovulation frequencies were available as well as

accurate estimates of the percentage of females that ovulate without subsequently implanting, it should be possible to predict pregnancy rates. This would be advantageous in years when samples were collected too early in the breeding season to directly observe pregnancies.

Temporal variation in sex ratios (Table 10) and age ratios (Table 12) suggests that these parameters should be estimated as close to the breeding season as possible for use in natality-rate estimates unless sampling biases increase during this period.

Litter size should be estimated from fetal counts late in gestation (to avoid including victims of prenatal mortality) or from placental-scar counts. If estimates are available from both early and late gestation, some additional data can be obtained. Comparisons of mean numbers of ova ovulated (based on corpus-luteum counts) with mean numbers of early implantation sites (embryonic swellings) provide an estimate of percentage loss of ova. Similarly, comparison of mean numbers of early implantation sites with late-gestation fetal counts yields an estimate of intra-uterine mortality rates. Presumably, if enough years of data were obtained covering periods of high and low coyote and prey densities, the relationships between coyote and prey densities and prenatal loss could be determined.

Finally, the above reproductive parameters should be subdivided into age-specific categories whenever possible. Special attention should be paid to the reproductive performance of pups (10-12 months

old) as this is the group most affected by changes in coyote and prey densities (Gier 1968, Knowlton 1972). In addition, when combining age-specific values to get a total population value, weighting with the appropriate age distribution may increase the accuracy of this estimate, especially if the age-specific values come from samples not representative of the actual age distribution in the population.

Annulus Formation

Annulus formation typically occurs during the winter months in many mammals. In some animals, such as deer and moose, annuli form during the first winter of life (Sergeant and Pimlott 1959, Low and Cowan 1963, and Wolfe 1969). In others (fox, bobcats, black bear, badgers, coyotes), the first annulus does not form or is not recognizable until the second winter of life (Sauer 1966, Linhart and Knowlton 1967, Lindzey 1971, Crowe 1972, Allen 1974, and Willey 1974).

There has been some speculation on the causes of annulus formation. Reduced food intake and subsequent lowered nutritional levels have been suggested as a factor that initiates annulus formation in deer (Low and Cowan 1963). In their work with deer, Low and Cowan noticed a thin annulus which they called a rut-line in close proximity to the main annulus. They conjectured that the rut-line might form as a result of reduced food intake during the rut; in addition they noted that levels of food intake might be associated with endocrine and/or photo-periodic phenomena.

Craighead et al. (1970) present evidence on grizzly bear, suggesting that annulus formation is not strongly correlated with nutritional levels. Annulus formation in this animal typically begins in late fall prior to denning activities. During this time, based on the quantity of body fat present, they are in a very high nutritional state. In fact, the light-staining cementum layer begins to form during the period of lowest nutrition (May and June) which is contrary to what would be expected if low nutritional levels stimulate annulus formation. They suggest that annulus formation is likely associated with endocrine processes. To my knowledge, no one has addressed this problem and, therefore, the mechanism of annulus formation remains largely unknown.

Age Assignment

Cementum-annulation counts provide accurate age data necessary for many population analyses. However, because of the time involved in tooth sectioning and staining, pups should be separated from older animals prior to this operation. I have previously described the rationale behind, and results of, my procedure which was based on the ratio of pulp-cavity cross-sectional length to tooth cross-sectional length.

Most predator population studies obtain the majority of their carcasses from hunters and trappers during the winter months (Gier 1968, Clark 1972, and Mathwig 1973). This period of carcass

collection coincides with annulus formation in canids (Linhart and Knowlton 1967, and Allen 1974). In coyotes, annuli apparently form during the winter and some may even separate from the periodontal membrane at this time.

Although my data do not conclusively prove or disprove the existence of "x" coyotes in this population, they do raise the question as to whether or not 1 year should be routinely added to the winter annulus count in the traditional method of assigning age. Until a large sample of known-aged coyotes or a late spring-early summer sample is obtained, this question remains unanswered. In addition, if the causative factors of annulus formation were known, they might help explain why annuli separate from the periodontal membrane earlier in some animals than in others. For example, if reproductive status, and hence endocrine status, affected annulus formation, then whether or not and when an animal became reproductively active might affect the timing of annulus formation.

Although I determined age distributions using both schemes (Table 11), in 2 of the 3 years they were not significantly different when tested by Chi-square. Nevertheless, this distinction should be made.

One other point not previously discussed is the reason for using longitudinal tooth sections. Occasionally, when tracing an individual annulus up the side of a tooth section, a split will occur and for a short distance it will appear as if there are two annuli. If cross sections

were taken at a point where an annulus had split, two annuli would be observed and the assigned age would be 1 year too old. Longitudinal sections allow the entire length of an annulus to be observed up both sides of the tooth.

Temporal Variation of Age Ratios

Few, if any, collection methods sample a population completely at random. Thus, potential biases in the sample age ratios should be evaluated. Because both fall-to-fall population mortality rates and birth-to-fall pup mortality rates are dependent on age-ratio estimates, age ratios should be estimated at the appropriate times.

In two instances I was unable to obtain samples at the needed time. I used the December sample age ratios to represent fall age ratios which are needed in the birth-to-fall pup mortality-rate calculations. Although these are my best estimates of fall age ratios, the pup percentages may be lower in December than in early fall since pup mortality is greater than adult mortality during the intervening time. Specifically, 28 percent of the tagged and/or transmitted coyotes were killed between September and the end of November (Table 23). This mortality was probably biased toward the inexperienced pups as previously discussed. But, I have also suggested that age ratios may not be changed very much by December. Nevertheless use of the December age ratios in these calculations probably overestimates

spring-to-fall pup mortality rates and underestimates annual mortality rates.

In the second case, December sample age ratios were used to approximate the May age ratios at the time of denning. These were used to convert the May pup population estimates to estimates of total population size (Table 19). The fact that over-summer pup mortality and differential fall pup mortality occurs, implies that the use of December age ratios in these calculations overestimates the actual May population size. I have attempted to correct for this problem by using the calculated May-to-fall pup mortality rate to estimate the age ratio of the previous May.

Population Density

The population trends indicated by the different density indices, were quite similar considering the small sample sizes involved. Each of the indices is potentially susceptible to different biases. For example, if the proportion of reproducing females or the timing of reproduction varied materially between years of different coyote densities, the denning index would not accurately reflect differences in densities. Since the trapping indices were probably biased toward pups, different catches between years might reflect the changes in percentage of pups more than changes in density. However, total population densities are significantly affected by, and related to, pup

densities. The results of the scat index are subject to biases introduced by such factors as differential degrees of vehicle travel on the index routes during the index period, different amounts of precipitation, or different levels of livestock grazing intensity between years.

In fact, any single relative index method is probably subject to biases of some kind. For this reason, it is desirable to establish as many independent indices as practical and then combine them into a composite (mean) index. The composite index should give a better estimate of population trends than a single index since its values should not be as subject to sampling error or individual biases as are the single indices.

The critical factor in my absolute density estimates was the size of the sample of spring-tagged pups. The small numbers of spring-tagged pups in the last 2 years and low recapture rates in all 3 years account for the extremely wide confidence intervals around the density estimates. In order to use this capture-recapture method and have narrow confidence intervals around the resultant estimates, it is imperative to mark larger samples in spring than I did during my study.

Mortality Rates

The two sets of mortality-rate estimates in this study were based on census and age ratio data in one case, and on a comparison of age ratios between seasons in the other. Since these mortality-rate

estimates are important in interpreting the observed changes in coyote densities, the potential biases in the data utilized must be adequately evaluated. The potential biases operating on the relative indices have previously been discussed. Age-ratio biases should not affect the annual population mortality rate estimates since the December age ratios are used each year in these estimates. Hence, the annual, population mortality rates should not be greatly affected by age-ratio biases. On the other hand, as previously described, the use of the December sample age ratios as being representative of fall age ratios probably overestimates birth-to-fall pup mortality rates.

Coyote Densities

Post-whelping density estimates on the study area in May ranged from 0.2 to 1.5 coyotes per square mile (0.1 to 0.6 coyotes per km²) for the capture-recapture procedure, and from 0.4 to 1.2 coyotes per square mile (0.2 to 0.5 coyotes per km²) for the capture-recapture estimates corrected with the index ratio estimator. I am assuming these density estimates apply to the shaded area in Figure 1 as well. These should be considered maximum density estimates because even the adjusted December age ratio probably underestimates the percentage of pups in the May population to some extent.

A number of other studies report estimated coyote densities (Table 25). I have listed these densities under two categories, pre- and

Table 25. --Coyote Densities in Curlew Valley and Other Areas

Study	Location	Method	Pre-whelping densities, Coyotes/km ²			Post-whelping densities, coyotes/mi ²		
			Minimum	Maximum	Mean	Minimum	Maximum	Mean
Present study	Curlew Valley	Capture-Recapture	0.1 ¹ (0.04) ²	0.8 ¹ (0.3)	0.4 ¹ (0.2)	0.2 ³ (0.08)	1.5 ³ (0.6)	0.7 ³ (0.3)
		Ratio estimation	0.2 ¹ (0.08)	0.6 ¹ (0.2)	0.3 ¹ (0.1)	0.4 ³ (0.2)	1.2 ³ (0.5)	0.7 ³ (0.3)
Clark (1972)	Curlew Valley	Capture-Recapture	0.1 ¹ (0.04)	0.3 ¹ (0.1)	0.2 ¹ (0.08)	0.4 ³ (0.2)	0.8 ³ (0.3)	0.6 ³ (0.2)
Gier (1968)	Kansas	Bounty calculations	--	--	0.7 ¹ (0.3)	--	--	2.0 ⁴ (0.8)
Knowlton (1972)	Texas	?	--	--	--	--	5-6 ⁵ (1.9-2.3)	0.5-1.0 ⁵ (0.2-0.4)
Mathwig (1973)	Iowa	Bounty calculations	--	--	0.7 ⁶ (0.3)	--	--	1.7 ⁴ (0.6)
Chessness (Personal Communication)	Minnesota	?	--	--	--	0.5 (0.2)	1.0 (0.4)	--
Nellis (1975)	Alberta	Aerial census	0.2 ⁶ (0.08)	1.1 ⁶ (0.4)	--	--	--	--

¹Whelping densities²Coyotes/km²³May densities⁴Immediate post-whelping densities⁵Fall densities⁶Winter densities

post whelping. Comparisons between studies are crude since most studies estimated densities at slightly different times of the year. Therefore, the effects of mortality between the times of estimation for each study results in values that are not directly comparable. However, since the estimates themselves are crude and do not reflect exact densities, rough comparisons between studies can perhaps be made.

I estimated the pre-whelping densities for Clark's study and my study by extending the capture-recapture data. In each year, the number of yearlings (13 months old) and adults in the May population was obtained by multiplying the total May population estimate of each method by the percentage of yearlings and adults in the estimated May age ratio. Since these estimates are subject to the same biases as the May population estimates, they should be considered as maximum pre-whelping estimates.

Mean pre-whelping densities in Curlew Valley were lower during Clark's study (0.08 coyotes per km²) than during my study (0.2 coyotes per km²). Cumulatively, the mean pre-whelping Curlew Valley densities were lower than those reported for Kansas coyotes (0.3 coyotes per km²) by Gier (1968) and for Iowa coyotes (0.3 coyotes per km²) by Mathwig (1973) (Table 25). Gier's (1968) estimates reflect breeding densities and Mathwig's estimates reflect late-winter densities which are presumably quite similar to breeding densities. Similarly, mean pre-whelping coyote densities (winter densities ranged from 0.08 to

0.4 coyotes per km²) on Nellis' (1975) Alberta study area, if given, would probably have also been greater than those in Curlew Valley.

As in the previous comparison, mean post-whelping (May) densities may have been greater during the years of my study (0.3 coyotes per km²) than during Clark's study (0.2 coyotes per km²) (Table 25). Post-whelping (May) densities were lower in Curlew Valley than those reported in all other studies except those occurring in Chesness' Minnesota study area (Personal Communication). He does not report a mean post-whelping density; however, based on his range of densities (from 0.2 to 0.4 coyotes per km²) his post-whelping densities apparently were quite comparable to those of Curlew Valley. The post-whelping densities reported by Gier (1968) of 0.8 coyotes per km² and by Mathwig (1973) of 0.6 coyotes per km² reflect the densities immediately following whelping, whereas the Curlew Valley values estimate May densities. Even if some allowances were made for post-whelping mortality, their estimated densities would probably still be greater than Curlew Valley densities.

Knowlton (1972) reported considerable variation in coyote densities in Texas. Although some areas in southern Texas averaged 1.9 to 2.3 coyotes per km², typical densities ranged from 0.2 to 0.4, which are more similar to those found in Curlew Valley. However, these Texas data reflect fall densities, hence post-whelping densities

would be somewhat greater and, therefore, would probably also surpass those found in Curlew Valley.

Curlew Valley densities were lower than those occurring in Kansas, Iowa, and Texas (Table 25). They may more closely approximate those occurring in more northerly areas (Minnesota and Alberta). If the pup percentage in May is greater than in my adjusted December age ratios, then even lower densities are implied. Regardless of whether or not this is true, during the course of the Curlew Valley studies coyote densities were probably lower than those reported for most other coyote populations.

Onset of Reproductive Activity Between Years

Analyses of ovarian and follicular changes throughout the winter, and comparisons between years, gave some insight into the timing of reproductive onset between years. Based on these data, I concluded that reproductive activity began earlier in all age classes in 1973-74 than in 1972-73.

There are several possible explanations for these observed differences. Coyote densities were considerably lower during the winter of 1973-74, the year in which reproductive activity began earlier, than during winter 1972-73. Therefore, these differences may be due to density-dependent pressures operating on the reproductive performance of the population. In years of high coyote densities, competition for food, mates, and denning sites may inhibit reproductive efforts by

many of the pups and subordinate animals. During periods of low densities, there is presumably less interaction between coyotes and conditions may exist which favor reproduction by pups and subordinate animals.

Another possibility concerns the relative severity of winter weather. The winter of 1973-74 was considerably milder than the winter of 1972-73 as revealed by meteorological data (Arlo Richardson, Personal Communication). Total snow accumulation in both winters was similar with accumulations of 59.7 and 56.9 inches (151.6 and 144.5 cm) in winter 1972-73 and 1973-74 respectively; however, 35.2 inches (89.4 cm) fell in December 1972 as compared to 19.6 inches (49.8 cm) in December 1973. Hence, pre-breeding winter weather was more severe in 1972 than in 1973. In addition, mean temperatures for the winter 1972-73 were considerably lower than those of winter 1973-74. In the first year temperatures averaged 4.1C, 4.2C, and 0.1C below normal for the months of December, January, and February, or averaged about 2.8C below normal during this period. During 1973-74, the mean December temperature was 1.8C above normal and January and February temperatures averaged 0.7C and 1.1C below normal. The mean temperature for this combined 3-month period did not deviate from normal in 1973-74.

Gier (1968) suggested that reproduction is adversely effected by severe winter weather. The effects of a severe winter in Kansas are even more drastic when coupled with low food availability. Although

food availability may well be an important factor in reproductive performance, fluctuations in the coyotes' major prey item did not seem to affect the onset of reproductive activity during the 2 years of my study since reproductive activity began earlier in 1973-74, during which time the jackrabbit density was lower than it had been in 1972-73.

I doubt that any single factor was responsible for these differences. Rather, a combination of factors probably influences the onset of reproductive activity in any 1 year.

Reproductive Rates

Ovulation Frequency

Age-specific ovulation frequencies for each year of my study are based on very small samples (Table 7). However, the samples of the "overall" data in each year are perhaps large enough to make meaningful comparisons and were statistically different only between 1972 and 1974. Nevertheless, ovulation frequencies may have increased each year.

Age-specific ovulation frequencies appeared to increase with age (Table 7); however, only the pup-yearling and pup-adult comparisons were statistically different. Approximately 63, 83, and 91 percent of the pups, yearlings, and adults in these samples ovulated during this period. Overall, 79 to 81 percent (depending on method) of the sampled coyotes ovulated.

This ovulation frequency is very similar to the rate of 84 percent reported by Clark (1972) for Curlew Valley coyotes. The mean ovulation frequencies reported for Curlew Valley coyotes are consistently higher than those reported in other studies (Table 26). Knowlton (1972) reported ovulation frequencies ranging from 48 to 81 percent with a mean of 62 percent for Texas coyotes. In another study, Linhart et al. (1968) reported 58 percent for New Mexico, 58 percent for Idaho, 42 percent for Arizona, and a mean for these three states of 56 percent.

Table 26. --Comparison of Ovulation Frequencies for Coyote Populations in Various Areas

Study	Area	% Ovulating and (Sample Size)		
		Minimum	Maximum	Mean
Present study	Curlew Valley	70 ¹ (50)	92 ¹ (25)	79 ¹ (128)
Clark (1972)	Curlew Valley	--	--	84 (19)
Knowlton (1972)	Texas	48 (29)	81 (21)	62 (123)
Linhart, et al. (1968) ²	New Mexico	50 (58)	70 (43)	58 (171)
" " "	Idaho	--	--	58 (19)
" " "	Arizona	--	--	42 (28)

¹See Table 7

²Based on calculations from only their untreated areas

Pregnancy Rates

Since the pregnancy-rate estimates (Table 8) were derived from the same carcass collections as were the ovulation-frequency estimates, comparison of pregnancy rates between years is also questionable. Sample sizes each year for the combined female category were comparable. The overall pregnancy rate (57 or 70 percent depending on method) in spring 1972 was apparently lower than in either spring 1973 (82 or 88 percent depending on method) or spring 1974 (88 percent). In addition, the 2-3 year totals suggest a marked increase in pregnancy rates as coyotes increase in age (Table 8).

Comparison of mean Curlew Valley pregnancy rates with those reported in other studies (Table 27) reveals trends similar to those of the ovulation-frequency comparisons. Carl Nellis (Personal Communication) reported that 72 percent of the females in his Alberta study area became pregnant, a rate quite comparable to that for Curlew Valley. In an average year, 48 to 50 percent of Kansas coyotes might become pregnant (Gier 1968) but considerable variation between years was noted (Table 27). Linhart et al. (1968) reported pregnancy rates for New Mexico coyotes ranging from 36 to 62 percent with a mean rate of 46 percent. Similarly, they reported pregnancy rates of 58 and 18 percent for Idaho and Arizona, respectively. Pregnancy rates of Texas coyotes ranged from 48 to 57 percent between areas with a

mean of 54 percent during the years of Knowlton's (1972) study. Collectively, these data suggest that in an average year in most North American areas, perhaps 50 percent of the entire female population becomes pregnant. Curlew Valley and Alberta coyotes appear to be exceptions.

Table 27.--Comparison of Pregnancy Rates for Coyote Populations in Various Areas

Study	Area	% Pregnant and (Sample Size)		
		Minimum	Maximum	Mean
Present study	Curlew Valley	57 ¹ (14)	88 ¹ (17)	77 ¹ (48)
Gier (1968)	Kansas	36 (-)	75 (-)	48-50 (-)
Linhart et al. (1968)	New Mexico	36 (28)	62 (21)	46 (171)
" " "	Idaho	--	--	58 (19)
" " "	Arizona	--	--	18 (28)
Knowlton (1972)	Texas	48 (29)	67 (21)	54 (123)
Nellis (Personal Communication)	Alberta	--	--	72 (-)

¹ See Table 8

Litter Sizes

The combined Curlew Valley intra-uterine litter sizes varied from 5.8 in 1973 to 6.7 in 1972 and had a mean value of 6.2 for this 3-year period (Table 9). Similarly, litter sizes weighted by the March-April age distribution varied from 5.7 in 1973 to 7.3 in 1972 with a mean of 6.2 for this 3-year period. The litter-size estimates reported in other studies are quite comparable to those observed in Curlew Valley (Table 28). Hamlett (1938) recorded mean litter sizes, based on embryo counts, of 6.6 for Utah and a mean figure of 6.2 based on 1,330 gravid females obtained from 13 western states. Both Gier (1968) and Knowlton (1972) reported greater variation in litter sizes than occurred in Curlew Valley; however, their samples were obtained from large areas encompassing many different environments and presumably different coyote densities. Both Gier's mean value of 5.6 and Knowlton's mean value of 5.4 were lower than that recorded in Curlew Valley.

Factors Influencing Coyote Reproductive Rates

A complex array of factors undoubtedly acts on reproductive rates which, in turn, influence the demography of coyote populations. Layne and McKeon (1956) suggest that the percentage of females becoming pregnant, the number of ova produced, the rates of fertilization

Table 28. --Coyote Litter-Size Comparisons in Various Areas

Study	Area	Litter Size and (Sample Size)		
		Minimum	Maximum	Mean
Present study	Curlew Valley	5.8 ¹ (19)	6.7 ¹ (15)	6.2 ¹ (42)
Gier (1968)	Kansas	4.8 (-)	6.4 (-)	5.6 (-)
Knowlton (1972)	Texas	4.3 (63)	6.9 (21)	5.4 ² (201)
Nellis (Personal Communication)	Alberta	--	--	5.8 (-)
Hamlett (1938)	Utah	--	--	6.6 (138)
" "	13 Western States	--	--	6.2 (1330)

¹See Table 9²Calculated from Knowlton's (1972) Table 4

and implantation, and the survival rate of embryos to parturition are four of the most important reproductive factors influencing total reproductive output or productivity of mammalian populations. Similarly, Knowlton (1972) suggests that the percentage of females capable of breeding, ovulation rates, implantation rates, and prenatal survival rates of embryos are all important in the coyote reproductive process. The last three points covered by both authors interact to determine ^{litter} ~~litter~~ size, hence these four parameters can be reduced to two major ones: pregnancy rates of females and litter size.

Knowlton (1972) suggests that although productivity can be increased by increasing litter sizes, perhaps the parameter having the greatest impact on productivity is the percentage of females becoming pregnant, particularly the pregnancy rate of pups (10 months old). Gier's (1968) observed variation in pup pregnancy rates supports Knowlton's claims. Gier suggests that anywhere from 0 to 65 percent of the pups may be capable of reproducing, depending on the conditions present in any 1 year, particularly severity of winter weather and food availability. The pup pregnancy rates estimated during my study also suggest considerable variation in the percentage of pups reproducing (Table 8).

Fluctuations in the availability of the food supply undoubtedly exert some effect on each of the four principal factors mentioned above. To my knowledge, Gier (1968) is the only author who has accumulated coyote reproductive data covering a sufficient length of time to have some insight into the effect food availability can have on coyote reproductive performance. However, the effects of food availability were not separated from those of weather. He states that in a good reproductive year (mild winter and high food availability), 65 percent of the pups and 83 percent of the older coyotes, or 75 percent of the entire female population would produce an average litter of 6.4 pups. In a poor year (severe winter and low food availability) none of the pups and only 60 percent of the older coyotes or 36 percent of all females might produce

an average litter of 4.5 pups. Reduced litter sizes presumably are achieved through reductions in each of the three previously mentioned prenatal stages: numbers of ova shed, implantation rates, and embryo survival. Thus, food availability and weather have a considerable effect on Kansas coyote populations.

Clark (1972) reported a positive relationship between coyote litter size and jackrabbit densities in Curlew Valley. Litter sizes reportedly varied from about 6.5 at lower jackrabbit densities to nearly 7.5 at higher jackrabbit densities. Although my data suggest some annual variation in litter sizes, they were not significantly different between years.

Although the role of nutrition has not been adequately tested under natural conditions, Gier's (1968) and Clark's (1972) data reveal some general patterns. Numerous experiments have been conducted on the effects of nutrition on reproduction in domestic livestock and white-tailed deer. Experiments on dairy and beef cattle and sheep suggest that lower levels of nutrition during periods of growth preceding puberty significantly lengthen the time before the test animals experienced their first estrus. Low levels of nutrition delayed puberty an average of over 7 months in four breeds of dairy and beef cattle (Joubert 1954). In another study, estrus was experienced by 26.4 percent of the ewe lambs that were fed additional amounts of food while on winter range, whereas only 13.6 percent of the control group entered

estrus (Burfening et al. 1971). Similarly, of 13 white-tailed deer yearlings maintained on low nutritional levels for a 6-week period prior to estrus, only 6 bred whereas all 8 of the yearlings subjected to maintenance nutritional levels bred (Verme 1969). The results of these studies reflect trends that are not too different from those reported by Gier (1968) for Kansas coyotes during years of differential food availability.

Presumably, food availability plays an important role in determining whether or not a coyote attains sexual maturity during the first year of life. Thus, the percentage of pups capable of reproducing would in fact have a major impact on the total reproductive output in any single year.

The effects of winter weather on coyotes in Kansas has already been mentioned. In addition, I have previously described the possible impact of winter weather on the onset of coyote reproductive activity. Clark (1971) also evaluated the effects of weather on coyote reproduction. By plotting mean unborn litter sizes against total December-to-February snowfall, he revealed an inverse relationship between litter size and snowfall. Litter sizes varied from about 7.7 in years of light snowfall (20-25 inches, 51-64 cm) to about 6.0 in years of heavy snowfall (70-80 inches, 178-203 cm). No relationship could be found between mean unborn coyote litter size and mean December-to-February temperatures. Clark (1971) suggested that both jackrabbit densities and winter weather interacted to affect coyote litter sizes.

The third major environmental factor presumably having a major influence on coyote reproductive performance is coyote density. The relatively low coyote densities in Curlew Valley (Table 25) may be causally related to both the high ovulation frequencies (Table 26) and pregnancy rates (Table 27) in the Curlew Valley coyote population. Similarly, litter sizes of Curlew Valley coyotes may have been somewhat larger than those reported in other recent studies (Table 28). Collectively, these data suggest that density-dependent processes may operate in coyote populations. Both the percentage of females capable of reproducing and litter sizes appear to be inversely related to coyote densities.

Several other canid studies have reported density-dependent responses of reproductive rates. Knowlton (1972) utilized records kept by coyote control personnel in Texas to relate coyote litter sizes to population density. With one exception, coyote litter sizes were inversely related to density in seven areas of South Texas included in his analysis. Average litter sizes varied from 4.3 in areas of high coyote densities to 6.9 in areas of low coyote densities. Although Knowlton did not directly relate pregnancy rates to coyote densities, he did suggest that litter sizes and pregnancy rates are probably similarly affected by various environmental factors.

In their study of the effects of stilbestrol on coyote reproduction, Linhart et al. (1968) sometimes found it difficult to determine whether

the observed low reproductive success was attributable to stilbestrol or to coyote density and other environmental influences. For example, increasing pregnancy rates of 20, 52 and 82 percent were documented in 3 successive years in one area of New Mexico. This area was treated with 7 and 9 stilbestrol tallow baits per square mile (2.7 and 3.5 per square kilometer) in 1963 and 1964 respectively. Thus treatments were similar in these 2 years. No stilbestrol was distributed in 1965. In this situation, coyote densities declined each year with corresponding increases in pregnancy rates. Irrespective of the factors causing this decline in densities, the comparison I wish to make is between decreasing densities and increasing pregnancy rates.

Layne and McKeon (1956) analyzing red fox density and reproductive data in various areas of New York, concluded that a slight inverse relationship existed between reproductive capacity and population density. But they admitted that population densities should be related to various environmental factors before the true relationships can be documented.

Finally, density-dependent processes also seem operative in wolf populations. Van Ballenberghe et al. (1975) suggested that human exploitation and subsequent reductions in density stimulated wolf productivity through increases in both the percentage of females breeding and litter size. As support for their conclusion they cited and contrasted the mean litter size of 6.0 and productivity of 2.67 pups per adult in

exploited, low-density Alaskan wolf populations (Rausch 1967) with similar values of 4.9 and 1.11 for the unexploited, high density Algonquin Park, Ontario wolf population (Pimlott et al. 1969).

In summary, no single environmental factor appears to influence coyote reproductive performance. Food availability, winter weather, and coyote densities may each affect reproduction to some extent. Presumably, these three factors interact with each other and others to determine the total reproductive output each year. The percentage of females becoming pregnant, particularly the percentage of animals reproducing in their first year, may be the most important factor in altering the reproductive performance of a population.

Age Ratios

I have assumed throughout this paper that there are fewer collecting biases associated with aerial gunning than with other collection procedures, primarily trapping and hunting. Presumably, it is more difficult for an adult to avoid an aircraft, once spotted, than to avoid traps or hunters. However, aerial gunners occasionally see coyotes at a great distance from their aircraft seeking the cover of dense patches of vegetation or brushy draws. Thus, the experienced adults may still have an advantage over the inexperienced pups in avoiding searching aircraft. Therefore, sample age ratios as determined from aerial-gunned carcasses are probably still biased toward pups. The extent of this bias is not known.

I have previously described the observed temporal variation in my sample age ratios (Table 12) and have discussed several possible explanations for this variation. If pups are killed at a greater rate, the percentage of pups in the actual population should decrease steadily throughout the winter rather than increase as my sample age ratios indicate (Table 12). This being the case, it may be impossible to obtain accurate estimates of winter age ratios. For the purposes of the following discussion I will use the percentage of pups in the overall age distributions (Table 11) to compare with the age ratios reported in other studies since most studies present only overall age ratios and do not discuss the effects of collecting biases or temporal variation on the sample age ratios. Knowlton (1972) was aware of the problems involved with accumulating age-ratio data over an extended period of time and attempted to avoid this problem by extracting samples from a given population in as short a time as possible.

The Curlew Valley age ratios in both studies were estimated from carcasses collected primarily from aerial gunning operations. Age ratios reported in other studies were estimated from sources other than aerial gunning, such as trapping, hunting, and coyote-getters (Table 29). Conceivably, different biases exist for each of the collecting techniques, making between-study comparisons crude at best. In addition, age-ratio comparisons are most meaningful when correlated with coyote densities and density trends.

Table 29. --Comparison of Coyote Winter Age Ratios

Study	Location	Source of carcasses	Percent Pups and (Sample Sizes)		
			Minimum	Maximum	Mean
Present study	Curlew Valley	Aerial gunning, hunting	42 (266)	56 (181)	48 (832)
Clark (1971)	Curlew Valley	Aerial gunning	56 (38)	71 (75)	69 (196)
Rogers (1965) ²	New Mexico	--	--	--	53 (137)
Gier (1968)	Kansas	Hunting, control operations	30 (--)	53 (--)	50 ¹ (--)
Knowlton (1972) ²	Texas	Coyote-getter kills	44 (--)	57 (--)	50 ¹ (--)
Mathwig (1973)	Iowa	Hunting, trapping	55 (67)	72 (72)	64 (139)
Chesness (Personal Communication)	Minnesota	Hunting, control operations	--	--	48 (212)

¹Approximate values²Fall age ratios

The age-ratio data in my study were extracted from the population following the last year of increase (49 percent pups) and first year of decrease (42 percent pups). In addition, the 1970-71 age ratio (56 percent pups) was obtained from the population following the third-to-last year of increase. Hence, the mean percentage of pups is based on 2 years of relatively high densities (1 year of increase and 1 year of decrease) and 1 year of low densities during a period of population increase.

Clark's (1971) minimum percentage of pups (56 percent) was obtained following the last year of population decline in Curlew Valley and therefore from a low-density population. Populations increased during the next 2 years and the sample winter age ratios were 68 and 71 percent pups. The low coyote densities in all 3 years plus the fact that the population increased in 2 of the 3 years may explain why Clark's (1971) pup percentages were greater than mine.

The only other study reporting pup percentages near those of Clark's was conducted in Iowa (Mathwig 1973) (Table 29). Mathwig attributes the high percentage of pups, in this high-density coyote population (Table 25), to intensive exploitation and suggests that the recent increase in numbers of bounty payments might reflect a gradual increase in coyote densities which would also explain the high pup percentages.

Knowlton's (1972) fall ratios were obtained from areas of high coyote densities and from relatively unexploited populations. Hence, his value of 50 percent pups probably reflects lower reproductive rates as compared to Clark's (1971) data.

Gier's (1968) estimated mean winter pup percentage (50 percent) was obtained from areas of relatively high coyote density (Table 25). Perhaps the great variation in pup percentages he observed between years is due to the substantial variation in reproductive rates.

Rogers (1965) reported a fall pup percentage in New Mexico of 53 percent; this percentage may have been somewhat lower by winter. Chesness (Personal Communication) reported an age ratio of 48 percent for Minnesota coyote populations. Densities were apparently low during this study (Table 25) but no population trend data were reported.

In summary, fall and winter age ratios are usually close to 50:50 (pups: yearlings and adults). The two studies (Clark's and Mathwig's) reporting substantially higher pup percentages sampled populations that were increasing. Generally speaking, high pup percentages might be found either in increasing coyote populations or heavily exploited populations. In both situations, high reproductive rates and/or high pup survival rates probably result in a high pup-to-adult ratio. High-density populations or decreasing populations might typically produce lower pup-to-adult ratios. These statements should be treated as extreme generalities since more than two or three factors

undoubtedly influence age ratios, and because of the potential collecting biases involved.

Mortality Rates

Annual Fall-to-Fall Population Mortality Rates

My estimates of annual population mortality rates are dependent on accurate composite-index and age-ratio estimates. Previous sections have dealt with the ways in which these data were obtained and the potential biases involved. I have concluded that although December sample age ratios do not exactly reflect early fall age ratios they may approximate them. Therefore, these annual mortality-rate-estimates can still be considered fall-to-fall estimates.

Extreme variation in annual mortality rates was observed during the 2 years of this study (Table 21). Coyote populations reached their highest densities in 1972 and by 1973 had declined to extremely low densities (Figure 20). Thus, the high estimated annual mortality rate during this period seems reasonable. By 1974, coyote densities had probably increased somewhat (Figure 20), perhaps due to the reduced annual mortality rate.

As stated earlier, it is in most cases statistically impossible to confirm changes in density during my study, nevertheless, by assuming that my estimates reflect actual changes in densities and by

comparing these density changes with changes in annual mortality rates, a suggestive relationship between mortality rates and changes in densities emerges. My estimated annual mortality rates are calculated, in part, from changes in density. Hence, some of the variation in mortality rates is directly attributable to the variation in coyote density. But since the mortality rates are also based upon fall age ratios which are independently determined, the annual mortality rates are partially independent of the indices.

Some knowledge of population densities and trends is helpful in interpreting mortality rates. The former is stated in most studies but due to the difficulty of obtaining reliable density estimates and the short duration of most studies, population trends are usually not discussed. For instance, had I obtained only one estimate of annual mortality rates, for example the 82 percent mortality rate for 1972-73, and reported it without relating it to population trends, I would have implied that Curlew Valley coyotes typically experience extremely high annual mortality rates. This, however, is not the case.

I will discuss the mortality rates reported in other studies but the problems of comparing them with each other and with the Curlew Valley estimates should be kept in mind. Knowlton's (1972) age distribution and subsequent mortality-rate estimations apply to relatively unexploited Texas coyote populations. He suggests that annual mortality rates of yearlings and older coyotes may exceed 40 percent

even in unexploited populations. I assume that the overall mortality rate (including pups) might exceed 50 percent in these populations. Knowlton's may be the only mortality-rate data available for unexploited populations.

Gier's (1968) mortality-rate estimates were apparently obtained from age distributions as determined by analyses of tooth wear and reproductive history. His age determination of young coyotes was probably accurate but age determination of old animals was probably less accurate. I have calculated approximate annual mortality rates from his Figure 15 (p. 49, 1968) in which he presents population fluctuations in a typical year. Based on this figure, 80 percent of the pups die in their first year of life, 52 percent of the yearlings and older coyotes die each year, and the annual mortality rate for the entire population is approximately 71 percent.

Alberta coyote populations are also heavily exploited (Nellis 1975). Nellis reports a pup mortality rate of 72 percent, a yearling rate of 58 percent, and rates thereafter of 40 percent or a mean annual mortality rate of about 63 percent.

Mathwig (1973) does not present mortality rates but concludes that they must be quite high since 64 percent of the coyotes collected during his study were pups, and 93 percent were under 3 years of age. There is heavy hunting pressure in southwest Iowa, where most of his carcasses were obtained, and he suggests that these age data imply a high mortality rate.

In a recent coyote population model utilizing some of Gier's (1968) and Knowlton's (1972) data as a basis for formulation; Connolly and Longhurst (1975) revealed that coyote populations, through compensatory reproductive responses, could withstand annual mortality rates of 70 percent without subsequent reductions in long-term mean population densities. In fact, even if 75 percent of the population was removed annually, it would take approximately 50 years to exterminate that population.

In an earlier study, Richards and Hine (1953) suggested similar compensatory capabilities of red fox populations in Wisconsin. Based on carcass analyses, they assumed that 2.55 young were produced per adult and that all females bred. With a potential productivity of 255 percent, a hypothetical red fox population would be capable of absorbing an annual mortality rate of 72 percent without subsequent reductions in mean annual population density. Although highly simplified and conjectural, these models suggest that coyote and red fox populations can withstand very high annual mortality rates; higher in fact, than most of those reported in actual field studies.

In conclusion, annual coyote mortality rates, whether in exploited or unexploited populations, typically exceed 50 percent and may vary considerably between years.

Birth-to-Fall Pup Mortality Rates

Accurate spring and fall age ratios are required for estimating pup mortality rates. The method of obtaining post-whelping age ratios has previously been described as have the problems and biases associated with obtaining estimates of these reproductive parameters. Since I have concluded in an earlier section that the December age ratios may approximate the fall age ratios, the mortality rates as calculated here may be reasonable estimates of birth-to-fall pup mortality rates. The calculated pup mortality rates (Table 24) follow the same trend as the annual population mortality rates (Table 21).

By varying the December age ratios it is possible to establish a range of mortality rates based on manipulations of the most questionable parameter in these calculations. The estimated post-whelping age ratio in spring 1973 was 2.43:1 or 71 percent pups (Table 24). If no birth-to-fall pup mortality occurred, a similar age ratio would be observed in the fall (for the purposes of this discussion I define the fall age ratio to be that which occurs in September). Thus, to attain a December age ratio of 0.69:1 (41 percent pups), a 72 percent $(\frac{2.43 - 0.69}{2.43})$ September-to-December pup mortality rate is implied. This mortality rate is inconsistent with the tag and transmitter return data previously discussed (Table 23). Therefore, some over-summer pup mortality probably occurred. If 50 percent of the September population is composed of pups, then a 59 percent $(\frac{2.43 - 1.0}{2.43})$ birth-to-September

pup mortality rate is implied. If 60 percent of the September population consists of pups, then a 38 percent $(\frac{2.43 - 1.5}{2.43})$ birth-to-September mortality rate is implied. Likewise, calculations using the same hypothetical age ratios and the 1974 data (Table 24) reveal similar changes in mortality rates.

If there were no birth-to-September pup mortality a September-to-December pup mortality rate of 41 percent would be implied, again inconsistent with tag and transmitter return data. September age ratios with 50 and 60 percent pups imply birth-to-September mortality rates of 59 and 38 percent respectively. These hypothetical age-ratio manipulations suggest that even if relatively high pup percentages occur in September, high birth-to-fall pup mortality rates are implied.

Additional evidence suggesting that some spring-to-fall pup mortality occurs was obtained from a comparison of first-winter return rates of spring and fall-tagged pups. I have previously calculated a May-to-September pup mortality rate of 13 percent using these data. Since this only estimates the mortality rate of pups from the time they are 5-6 weeks old, the birth-to-fall mortality rate would likely be greater than 13 percent.

During May 1973, we trapped coyotes in order to increase the number of transmitted animals available for summer mortality studies. Of the 7 females caught, 5 were dry (not lactating). Nursing females may have been underrepresented as they may not be as

active (vulnerable) during this time as dry females. These dry females might have included females that never ovulated, females that ovulated but failed to implant, females that ovulated and implanted but lost their litters in utero, or females that ovulated, implanted, and gave birth but subsequently lost their litters. Females in this last category cannot be recognized in the March-April carcass analyses nor in the subsequent December placental-scar analyses.

Indirect evidence implying high birth-to-fall mortality rates comes from a comparison of Curlew Valley pregnancy rates (Table 27), litter sizes (Table 28) and fall age ratios (Table 29) with those of other studies. The Curlew Valley coyote population experienced substantially higher pregnancy rates than reported in most other studies as well as having had somewhat larger litter sizes. Therefore, post-whelping age ratios should consist of higher pup percentages than those in other areas. But, by fall and/or winter, the percentage of pups in the Curlew Valley age ratios were very similar to those reported in other studies. Therefore, higher birth-to-fall pup mortality rates apparently occurred in Curlew Valley during my study than elsewhere.

Gier (1968) suggests that in poor reproductive years, if conditions remain unfavorable into the summer, a high percentage of the pups would die. In good reproductive years in which conditions remain favorable into summer, a high pup survival rate would be expected.

Thus he observed considerable yearly variation in birth-to-fall pup mortality rates in the same populations.

Knowlton (1972) suggested that in Texas some post-whelping pup mortality occurs but that the mortality of very young pups is low. His speculations involved a hypothetical unexploited population that had stabilized with respect to the environment.

Several other studies report high rates of post-natal juvenile mortality. Nellis et al. (1972) report that during 3 consecutive years of low snowshoe hare (Lepus americanus) densities, no juvenile lynx (Lynx canadensis) were recruited into the fall populations. They indicated that during their study female lynx conceived regardless of snowshoe densities. Juvenile mortality, and not the failure to conceive, was the primary factor limiting productivity of this lynx population during years of low snowshoe densities. They compared their conclusions with those of Macpherson (1969) whom they cited, who studied arctic fox (Alopex lagopus) populations in Canada. He too observed a year in which no pups were weaned and concluded that arctic fox productivity was a function of post-natal pup mortality as related to food abundance.

Similarly, Rausch (1967) accumulated data on exploited Alaskan wolf populations which indicated that a high proportion (89 percent, $n = 89$) of the females 2 years old and older ovulated, conceived, and probably gave birth. He concluded that variation in the percentage of

pups in the fall age ratio was a function of in-utero and post-natal pup mortality. He estimated birth-to-winter pup mortality rates of from zero to 60 percent, depending on areas. Van Ballenberghe et al. (1975) reported a pup mortality rate of 56 percent in the first 7 months of life for an exploited wolf population in northeastern Minnesota. In addition, they calculated a maximum pup mortality rate of 57 percent in the first 7 months of life for the unexploited wolf population in Algonquin Park, Ontario, based on data presented by Pimlott et al. (1969). They concluded that wolf pups surviving their first few weeks of life probably have a good chance of surviving up until about 6 months of age and that food availability may be a major factor influencing post-natal pup mortality.

Storm et al. (1976) speculated on the causes of lower recovery rates for red fox pups of large litters than of small litters. They suggested that this was a result of higher over-summer pup mortality rather than reduced vulnerability. Among other reasons, they suggested that increased energy demands placed on the adults by large litters and perhaps an increasing intensity of competition among pups might account for these lower survival rates. By analogy I suggest that even average size litters, during a period of low food availability or whenever any other factor adversely affects the ability of adults to supply the energy demands of the litter, could experience increased post-natal pup mortality.

Anderson (1957) reports data on pup mortality in a beagle kennel. Because of the importance of sound nutrition, the beagles' diets were excellent, thus eliminating the effects of poor nutrition. No special care was given to the females or litters in order to obtain information on the natural incidence of pup mortality. His study spanned 4 years and was based on 234 litters numbering 1,157 pups. He reports a 29.4 percent pup loss up to weaning (6 weeks of age). Of the pups dying during this period, 82 percent died during the first week of life. The major periods of mortality occurred during transitional changes, specifically at birth and to a lesser extent again at weaning. He cites two other dog studies reporting losses of pups up to weaning and 8 weeks of age of 32 percent (Clive McCay, Personal Communication) and 34 percent (Rowlands 1950) respectively. On the basis of these data he concludes that normal kennel operations should expect to lose about one-third of the pups during the first 6 to 8 weeks of life. Similarly, Scott (1967) suggested that a kennel operation with a 15 percent post-natal pup loss was a good operation. He mentioned that some breeds normally have even higher rates of pup loss.

Two additional points should be mentioned. First, Anderson (1957) does not mention losses of entire litters which contrasts with my speculation concerning pup losses. Secondly, he presents data on pup mortality rates for different aged females. The mortality rate of pups decreases in magnitude between young females and 3 year-old females and increases steadily in litters of females 4 years of age and older.

The rates of pup loss are higher for 4 year old and older females than in any of the preceding age classes. This could have implications for coyote productivity. For instance, a heavily exploited coyote population, composed of younger coyotes, should according to this scheme, suffer lower birth-to-May pup mortality rates than an unexploited or lightly exploited population, composed of a greater percentage of older coyotes. This, of course, assumes other conditions are similar between populations and that coyotes behave similarly to dogs.

Some additional data relevant to this discussion was obtained from two studies of reproduction in white rats. Richter and Barelare (1938) gave 10 female rats free access to unlimited amounts of food and measured their caloric consumption during a 1 month period prior to mating, during gestation, and during lactation. The mean number of calories required per day increased from 45.3 before mating, to 59.8 at the end of gestation, to 118.3 at the end of lactation. Another study (Babcock et al. 1940) followed two groups of rats throughout their reproductive life. One group was allowed to nurse their young while the other group was not. The females that were not allowed to nurse their young weighed more and gave birth to nearly one-half again as many litters as did the females in the other group. Both of these studies indicate that the energy demands upon the female are much greater during lactation than during gestation. Similar patterns may also operate in coyote populations.

Coyotes probably have a baseline post-natal mortality rate just as do domestic dogs. It seems reasonable to assume that any postnatal pup mortality in excess of this "expected" mortality rate, excluding that due to an outbreak of disease, unusually severe weather, or other unusual conditions may be due to the females' inability to meet the increased energy demands of gestation and particularly lactation. I have previously suggested, as have other studies, that the condition of the female during proestrus is extremely important in determining whether or not the female breeds. I suggest that in years of low food availability and/or high coyote densities, with presumed accompanying increases in stress, that a greater percentage of those females successfully breeding may be in poorer condition than in years of high food availability and/or low or increasing coyote densities. Of the females breeding, those in poorest condition could be expected to encounter increasing energy problems as gestation proceeds resulting in some in-utero pup mortality. As the energy requirements increase during lactation, accelerated pup losses and perhaps losses of entire litters might occur. Hence, during these years, increased pre-and post-natal pup mortality could be expected.

In summary, there can be considerable variation in pup mortality rates during the first 4 to 5 months of life. In years of high coyote densities and/or low food supplies, or in years of population decline, a relatively high post-whelping pup mortality might occur.

During years of population increase, the increase may in part be due to reduced birth-to-fall pup mortality.

Analyses of Demographic Patterns

Analyses of the data collected during this study allow speculation on the factors producing the demographic patterns observed in the Curlew Valley coyote population. Much of the following discussion is speculative in nature and is based on results obtained from small sample sizes. If more data were available, these preliminary interpretations could easily change.

The reproductive samples used to estimate pregnancy rates were small in each year. In spite of these small samples, the annual pregnancy rates follow a trend. The highest coyote densities occurred in 1972 (Figure 20), and breeding density was highest that spring (Figure 15). The jackrabbit population was quite high in spring 1972 as revealed by an index value of 87 compared to the highest index value (130) recorded during the jackrabbit study (L. Charles Stoddart, unpub.). It declined in each successive year as evidenced by spring index values of 18 and 6 in 1973 and 1974. Thus, pregnancy rates were lowest in a year of high coyote densities and fairly high jackrabbit densities. During years of lower coyote densities and lower jackrabbit densities (1973 and 1974) pregnancy rates were considerably higher. The pregnancy rate of pups, not surprisingly, appeared to vary more than those

of the other age groups. Although my samples are small, coyote density may have been a greater force in affecting pregnancy rates than jackrabbit density.

Analysis of the mortality rates also gives some insight into the demographic patterns of this population. In fact, a combination of annual population and birth-to-fall pup mortality rates accounts for much of the observed changes in population densities. It should be kept in mind that the annual mortality rates are in part determined by these changes in densities between years.

Nevertheless, the extreme reduction in densities between 1972 and 1973 was probably largely a result of high annual and post-natal pup mortality rates during this period. Based on the temporal distribution of coyote mortality (Table 21) the annual mortality occurred between fall 1972 and spring 1973. The reduced density in spring 1973 may have prompted a higher pregnancy rate; however, this initial increase in productivity may have been offset by the high birth-to-fall pup mortality rate of 72 percent (Table 24).

Coyote densities may have been similar between spring 1973 and spring 1974 (Figure 15, Table 15). Similarly, pregnancy rates were quite similar between these 2 years (Table 8). Thus the total reproductive output may have been similar between the springs of 1973 and 1974. If this was the case, then some factor other than reproduction is necessary to explain the assumed increase in density in 1974,

although the densities in these 2 years were not statistically different. The annual mortality rate between 1973 and 1974 was half that of the previous period. Similarly, a higher percentage of pups produced in spring 1974 probably survived to fall 1974. Therefore, the increased coyote density in 1974 was likely due to reduced mortality rates. Thus, variations in mortality rates apparently had more of an impact on changes in population densities than did variations in reproductive rates during the period of my study.

Some speculation on the causes of these changes in mortality rates seems in order. As discussed previously, most of the mortality of animals 5 months old and older has been man-induced during my study. Thus variations in the intensity of exploitation are probably responsible for the observed variation in mortality rates. The high coyote densities in 1972 may have been partly responsible for the high annual mortality rate between 1972 and 1973. Perhaps during years of high densities, a greater percentage of coyotes are unable to establish territories easily and, therefore, spend more time exploring unfamiliar terrain. Because of this, a greater percentage of coyotes are more vulnerable to man-induced mortality by lacking knowledge of available escape routes and cover. Thus, a greater percentage of coyotes might be removed by man's activities. A greater rate of exploitation may not necessarily imply increased hunting pressure, but rather increased hunting success.

The decreased annual mortality rate between 1973 and 1974 might be a function of the lower coyote densities during this period. Coyotes may have been more successful in establishing territories earlier in this winter and, therefore, exposed themselves to new territory only during home-range expansion activities as previously discussed. They would, therefore, be in familiar territory a greater percentage of the time and would be somewhat less vulnerable to man's activities.

Winter severity may also have had some effects on man-induced coyote mortality rates. Winter temperatures in 1972-73 were more severe than in 1973-74. Although total snowfall differed little between years, the amount received in December 1972 (35.2 inches, 89.4 cm) was nearly twice that of December 1973 (19.6 inches, 49.8 cm). Hence, severe weather occurred earlier in 1972-73 than in 1973-74 (Arlo Richardson, Personal Communication). The energy demands of coyotes undoubtedly increase with colder temperatures. Therefore, coyotes may spend relatively more time searching for food and consequently expose themselves more to man's activities during severe winters than during mild winters. This may partially account for the high mortality rate during winter 1972-73. Milder winter weather and resultant lower energy demands may have been a force behind the substantially lower mortality rate observed during the second winter, 1973-74. Increasing the complexity of the situation is the fact that jackrabbit availability

decreased between winters. Thus, even though energy demands may have been lower than in the first winter, coyotes may have had to search as long or longer to meet these demands in the second winter.

Coyote density and energy demands may thus be two of the major factors that interact with each other as well as with other factors to influence the magnitude of coyote mortality rates in any single year.

Almost nothing is known about the factors responsible for early pup mortality. Nevertheless, these mortality rates followed patterns similar to those of the annual population mortality rates. Therefore, pup mortality rates may be related to coyote densities in some manner.

Gier (1968) mentioned low food availability, parasites and disease, and rainy weather as being some of the factors responsible for high rates of post-natal pup mortality. I have no data on the parasites and diseases that may affect coyote pups in Curlew Valley. Late spring and summer weather is typically quite dry in Curlew Valley, hence I am discounting weather as an influence on pup mortality rates. Although food availability is probably an important factor, the 2 years for which I have pup mortality-rate estimates show no positive relationship to jackrabbit density. However, there was an inverse relationship between these two parameters. Thus, differences in jackrabbit availability apparently cannot account for the observed differences in pup mortality rates during this study. This conclusion is in direct contrast with results of other predator studies previously discussed

(Rausch 1967, Gier 1968, Macpherson 1969 as cited by Nellis et al. 1972, Nellis et al. 1972, and Van Ballenberghe et al. 1975). I suspect this contrast may be due to incorrect inferences drawn from only 2 years of data. Perhaps if more data were available from a wider range of coyote and jackrabbit densities, a clearer, more logical pattern would emerge.

Perhaps coyote density has some influence on the ability of females, particularly the yearlings (12 months old), to successfully raise litters. As discussed above, an average of 13 percent of the pups die between May and September. I have also suggested that during my study from 32 to 68 percent of the pups died within the first 6 to 8 weeks of life. If most litters lost from 32 to 68 percent of the pups prior to May, small litter sizes should have been encountered during our denning efforts. This, however, was not the case. The mean denned litter size (6.2) in 12 dens (1972, 1973, and 1974 combined), in which all pups were accounted for, was identical to the mean litter size determined from carcass analyses (Table 9). Hence during this study, birth-to-May pup mortality apparently occurred primarily through the loss of entire litters rather than of a few individuals from each litter although losses in this last category undoubtedly contributed to the mortality rate. The inexperienced yearlings (12 months old) might be the age group involved, especially if the stresses of high densities affect them more than older females.

The pregnancy-rate estimates in the 3 years for which I have data do not differ statistically (Table 8). Similarly, a comparison of estimated percentages of females ovulating during my study with the one estimate obtained during Clark's (1972) study shows little difference between years (Table 26). Admittedly, the sample sizes are small, but nevertheless, these data suggest that although reproductive rates may have varied a little between years, these variations were not as extreme as those reported by Gier (1968) and Knowlton (1972). Annual mortality rates and post-natal pup mortality rates may have been largely responsible for the observed variations in coyote densities during this study. In this respect, the Curlew Valley coyote population may have behaved somewhat like the previously mentioned lynx and arctic fox populations.

Coyote productivity and subsequent juvenile recruitment probably were altered by variations in both reproductive performance and post-natal pup mortality. Annual population mortality and movements are the other two factors which interact with productivity to effect changes in the demographic patterns of coyotes. These population processes are in turn affected by variations in environmental characteristics such as food availability, coyote densities, and weather.

2-3-Year Population Simulation

In previous sections I have discussed at length both the potential biases that might affect my data and the shortcomings of these data. I developed a population simulation to test the reliability of these data but due to some characteristics of this simulation the reliability of only three estimates (fall age ratios, relative indices, and annual mortality rates) could be tested.

The reliability of these estimates could conceivably be tested by applying the reproductive and mortality data to a hypothetical population beginning in 1972 and allowing the ensuing population fluctuations to occur through 1974. The May 1972 capture-recapture estimate of the number of pups on the study area was used as the starting point (Figure 21), thus allowing comparisons of the subsequent, simulated May pup populations with respective capture-recapture estimates.

The first step in simulation involved applying a May-to-September pup mortality rate of 13 percent to the May 1972 pup population. This established the number of pups in September 1972. By applying the December age ratios to the number of pups in September, the total population size and number of yearlings and adults (by subtraction) in September 1972 was obtained. The annual population mortality rate was applied to the total fall population to obtain the population size in March-April, 1973. This assumes no yearling and adult mortality

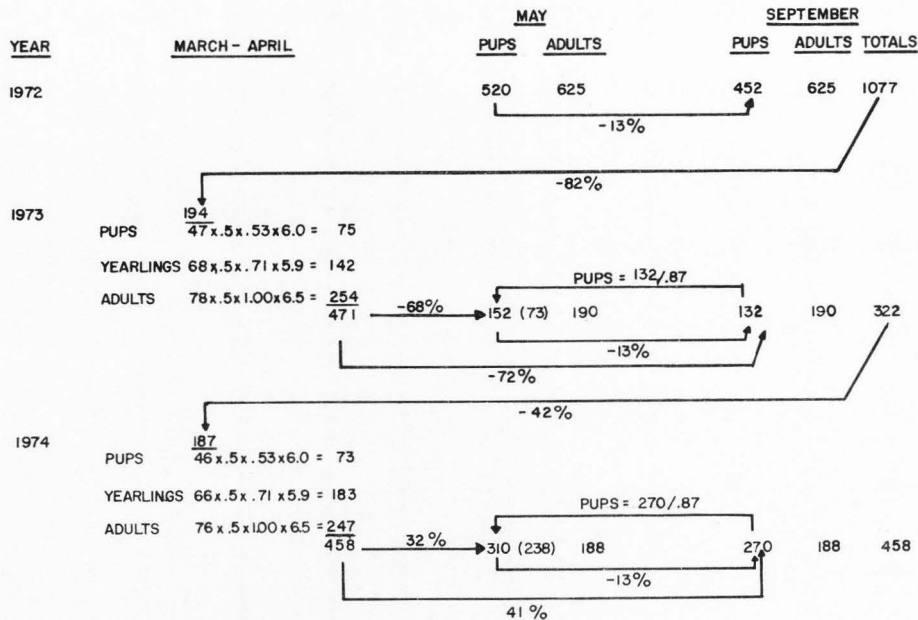


Figure 21. Three-year simulation of Curlew Valley coyote population.

between spring and September (Table 23), an assumption that is violated to some extent, as I have indicated that some mortality does occur, although I assume it is minimal. The March-April age distribution was applied to the estimated population size in order to obtain the numbers of pups (10 months old), yearlings (20 months old), and adults in the 1973 pre-whelping population. Age-specific sex ratios (Table 10), pregnancy rates (Table 8), and litter sizes (Table 9) were applied to each age group to obtain the number of pups produced by each age group. The total number of pups at birth (1973) was reduced by the estimated birth-to-September (1973) pup mortality rate. This established the number of pups present in September 1973 and application of the appropriate December age ratio yielded the number of yearlings and adults and total population size in September 1973. By assuming that 13 percent of the pups died between May and September, the number of pups in September 1973 was used to estimate the number of pups that would have been present in May 1973. The same procedure was utilized to obtain the various population estimates in 1974.

The assumption of no yearling and adult mortality over summer automatically equates the number of animals in the pre-whelping March-April population to the number of yearlings and adults in the subsequent September population. Because of this, the number of pups in September is also automatically established by way of the fall age ratio. Therefore, regardless of the total number of pups produced by the

March-April population and hence regardless of the post-whelping age ratio the number of pups in September will remain constant by way of changes in birth-to-fall pup mortality rates since the December age ratio does not change. Hence, this simulation does not validate estimates of the March-April age distributions, sex ratios, pregnancy rates, litter sizes, post-whelping age ratios, or birth-to-fall pup mortality rates.

This simulation does however add some support to the relative-index, fall (December) age-ratios, and annual mortality-rate estimates. The relative indices and fall age ratios, both independently determined, were used to estimate annual mortality rates which I in turn utilized to reduce the September populations to subsequent March-April populations. The fall age ratios allowed determination of the numbers of pups in September which, when corrected for a 13 percent May-to-fall pup loss, established the numbers of pups present in the May populations. If the index and/or fall age ratio estimates had departed substantially from the actual population parameters, then the sizes of the September populations and/or annual mortality rates would have varied resulting in variations in the number of animals in the subsequent March-April populations. For example, if the calculated 1973 March-April population had been larger than 194, then by way of the fall age ratio, the September pup population would also have been larger. This would result in a larger calculated May pup population that would depart even

more from the capture-recapture May pup estimates (1973). On the other hand, age ratio changes resulting in a smaller September population or age ratio and index changes resulting in a higher annual mortality rate in 1972-73 would, by similar processes, yield a smaller calculated May pup population which would be closer to the May 1973 capture-recapture pup estimate.

The validity check consists of comparing the simulated numbers of pups present each year in May (Figure 22) with respective capture-recapture estimates of pup numbers each May. The comparison cannot be made in 1972 for obvious reasons. The calculated number of pups in May 1973 (152) was twice that of the capture-recapture estimate (73). Although this is not good agreement, the May capture-recapture pup estimates were bracketed by wide 95 percent confidence intervals (Table 19). The comparison between the two pup estimates in May 1974 shows much better agreement. The fact that the simulated May pup estimates and the capture-recapture May pup estimates agree as closely as they do (Figure 22) suggests that the relative-index, fall age-ratio, and annual mortality-rate estimates obtained during this study may be realistic.

Summary

Various parameters of a northern Utah-southern Idaho coyote population were studied on the 1,813 km² Curlew Valley study area and

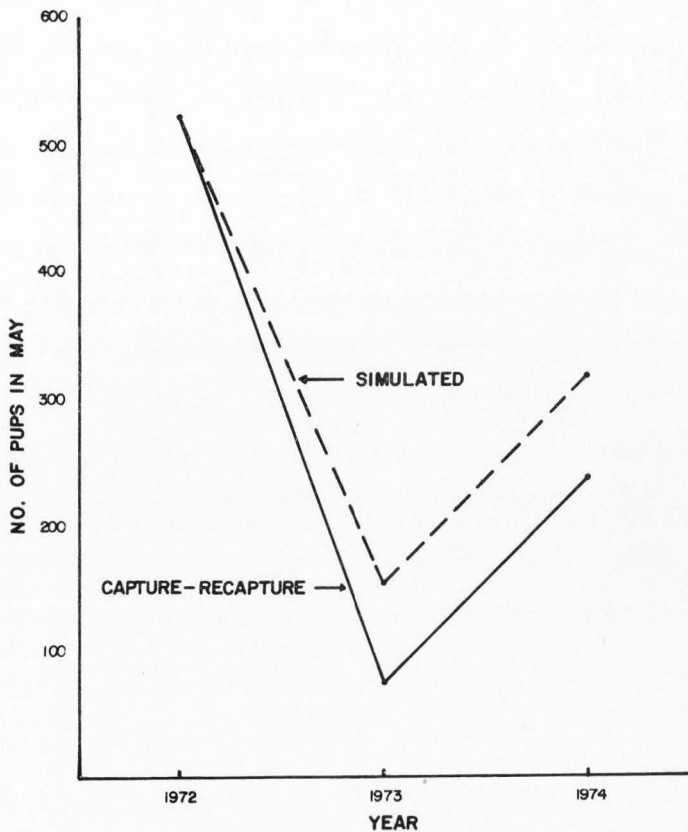


Figure 22. Comparison of the estimated (capture-recapture) and simulated numbers of pups in May.

surrounding areas from August 1972 through September 1974. I estimated relative densities by conducting spring-denning, fall-trapping, and fall scat-line operations. Absolute densities were estimated by mark-recapture procedures, employing data obtained from the spring-denning and fall-trapping operations. Carcass analysis provided estimates of sex and age ratios, ovulation frequencies, pregnancy rates, and litter sizes. Combinations of relative-index data and fall age ratios provided estimates of annual fall-to-fall population mortality rates and seasonal age-ratio comparisons yielded estimates of birth-to-fall pup mortality rates. Telemetry and tagging studies supplied information on the causes and seasonal distribution of coyote mortality.

A careful review of cementum aging suggests that mammals collected during the period of annulus formation should be aged with caution. It may be possible to collect two animals, both of the same age, that display different numbers of annuli.

Reproductive analyses suggested that the timing of reproductive activity varied between years. Coyote densities may have had a greater impact on the onset of reproductive activity than did densities of their major prey item, the black-tailed jackrabbit. Mean ovulation frequencies and pregnancy rates for the entire female population varied between years. Ovulation frequencies varied from 70 to 92 percent and pregnancy rates ranged from 57 to 88 percent. Ovulation frequencies and pregnancy rates appeared to be inversely related to coyote densities

rather than to jackrabbit densities. Similarly, age-specific ovulation frequencies varied from 63 percent (pups) to 91 percent (adults) and pregnancy rates varied from 53 percent (pups) to 100 percent (adults). Whenever possible, reproductive estimates should be analyzed in an age-specific manner. Overall reproductive estimates should be obtained by weighting age-specific values with respective age-distribution frequencies whenever possible.

Both the relative-and absolute-density data revealed substantial short-term variation in coyote densities. Post-whelping, May coyote densities may have varied from 1.5 to 0.2 coyotes per square mile ($0.6-0.08 \text{ coyotes/km}^2$) in consecutive years. Curlew Valley coyote densities appear to be lower than those occurring in Texas, Kansas, and Iowa and are perhaps more comparable to those occurring in more northerly latitudes (Minnesota and Alberta).

The percentage of pups in the winter age ratios of Curlew Valley coyotes varied from 42 to 56 percent. The mean value of 48 percent was similar to those reported in most other studies. However, they were substantially lower than those reported for Iowa (Mathwig 1973) and an earlier Curlew Valley study (Clark 1972). These differences, at least between the two Curlew Valley studies, can probably be explained on the basis of different population trends during these two studies.

Mortality of coyotes 5 months old and older was almost entirely man-induced as only 1 of 52 transmitter recoveries was a result of

natural mortality. Annual fall-to-fall population mortality rates varied from 42 to 82 percent, probably resulting from differential rates of human exploitation which may have been related to varying degrees of coyote vulnerability at different coyote and jackrabbit densities.

Natural mortality factors were presumably responsible for most of the pup mortality occurring between birth and fall. Estimated birth-to-fall pup mortality rates varied from 41 to 72 percent with perhaps the major losses occurring between birth and May. The higher-than-average pregnancy rates of Curlew Valley coyotes suggests a high post-whelping pup-to-adult age ratio, higher than would be expected in the other studies discussed. Therefore, the similarity of Curlew Valley winter age ratios during my study and those reported in most other studies, implies a high birth-to-fall pup mortality rate. The over-summer pup mortality rates reported in this study are within the range reported in studies of other carnivorous mammals. During the period of this study, mortality rates apparently were more influential than reproductive rates in determining population trends.

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